

ANN

QL  
7  
R454  
NH

de la  
SOCIÉTÉ SUISSE DE ZOOLOGIE  
et du  
MUSÉUM D'HISTOIRE NATURELLE  
de la Ville de Genève

tome 113  
fascicule 2  
2006

SWISS JOURNAL OF ZOOLOGY

REVUE SUISSE DE ZOOLOGIE

# REVUE SUISSE DE ZOOLOGIE

## TOME 113—FASCICULE 2

Publication subventionnée par:  
ACADÉMIE SUISSE DES SCIENCES NATURELLES (SCNAT)  
VILLE DE GENÈVE  
SOCIÉTÉ SUISSE DE ZOOLOGIE

DANIELLE DECROUEZ  
Directrice du Muséum d'histoire naturelle de Genève

ALICE CIBOIS, PETER SCHUCHERT  
Chargés de recherche au Muséum d'histoire naturelle de Genève

### *Comité de lecture*

Il est constitué en outre du président de la Société suisse de Zoologie, du directeur du Muséum de Genève et de représentants des instituts de zoologie des universités suisses.

Les manuscrits sont soumis à des experts d'institutions suisses ou étrangères selon le sujet étudié.

La préférence sera donnée aux travaux concernant les domaines suivants: biogéographie, systématique, évolution, écologie, éthologie, morphologie et anatomie comparée, physiologie.

### *Administration*

MUSÉUM D'HISTOIRE NATURELLE  
1211 GENÈVE 6

Internet: <http://www.ville-ge.ch/musinfo/mhng/page/rsz.htm>

### PRIX DE L'ABONNEMENT:

SUISSE Fr. 225.—

UNION POSTALE Fr. 250.—  
(en francs suisses)

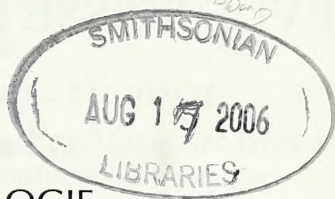
Les demandes d'abonnement doivent être adressées  
à la rédaction de la *Revue suisse de Zoologie*,  
Muséum d'histoire naturelle, C.P. 6434, CH-1211 Genève 6, Suisse



ANNALES

de la  
SOCIÉTÉ SUISSE DE ZOOLOGIE  
et du  
MUSÉUM D'HISTOIRE NATURELLE  
de la Ville de Genève

tome 113  
fascicule 2  
2006



SWISS JOURNAL OF ZOOLOGY

REVUE SUISSE DE ZOOLOGIE

# REVUE SUISSE DE ZOOLOGIE

## TOME 113—FASCICULE 2

Publication subventionnée par:  
ACADÉMIE SUISSE DES SCIENCES NATURELLES (SCNAT)  
VILLE DE GENÈVE  
SOCIÉTÉ SUISSE DE ZOOLOGIE

DANIELLE DECROUEZ  
Directrice du Muséum d'histoire naturelle de Genève

ALICE CIBOIS, PETER SCHUCHERT  
Chargés de recherche au Muséum d'histoire naturelle de Genève

### *Comité de lecture*

Il est constitué en outre du président de la Société suisse de Zoologie, du directeur du Muséum de Genève et de représentants des instituts de zoologie des universités suisses.

Les manuscrits sont soumis à des experts d'institutions suisses ou étrangères selon le sujet étudié.

La préférence sera donnée aux travaux concernant les domaines suivants: biogéographie, systématique, évolution, écologie, éthologie, morphologie et anatomie comparée, physiologie.

### *Administration*

MUSÉUM D'HISTOIRE NATURELLE  
1211 GENÈVE 6

Internet: <http://www.ville-ge.ch/musinfo/mhng/page/rsz.htm>

### PRIX DE L'ABONNEMENT:

SUISSE Fr. 225.—

UNION POSTALE Fr. 250.—  
(en francs suisses)

Les demandes d'abonnement doivent être adressées  
à la rédaction de la *Revue suisse de Zoologie*,  
Muséum d'histoire naturelle, C.P. 6434, CH-1211 Genève 6, Suisse



## **Descriptions of three new *Platypalpus* Macquart from Guangdong, China (Diptera, Hybotidae, Tachydromiinae)**

Ding YANG<sup>1,2</sup>, Bernhard MERZ<sup>3</sup> & Patrick GROOTAERT<sup>4</sup>

<sup>1</sup> Department of Entomology, China Agricultural University, Beijing 100094, China.

E-mail: dingyang@cau.edu.cn

<sup>2</sup> Key Lab of Insect Evolution & Environmental Changes, Capital Normal University, Beijing 100037, China.

<sup>3</sup> Département d'Entomologie, Muséum d'histoire naturelle, C. P. 6434, CH-1211 Genève 6, Switzerland.

E-mail: bernhard.merz@ville-ge.ch

<sup>4</sup> Department of Entomology, Royal Belgian Institute of Natural Sciences, Vautierstraat 29, 1000 Brussels, Belgium.

E-mail: Patrick.Grootaert@naturalsciences.be

**Descriptions of three new *Platypalpus* Macquart from Guangdong, China (Diptera, Hybotidae, Tachydromiinae).** - *Platypalpus* Macquart is recorded for the first time from Guangdong province. Three new species are described as new to science: *P. convergens* sp. n., *P. guangdongensis* sp. n., *P. zhangae* sp. n. A key to the species of the genus from Guangdong is presented.

**Keywords:** Hybotidae - Tachydromiinae - *Platypalpus* - Guangdong - new species.

## **INTRODUCTION**

The genus *Platypalpus* Macquart belongs to the subfamily Tachydromiinae of the family Hybotidae. It is easily identified by the following combination of characters: eyes narrowly separated on frons and face, mid leg raptorial, and anal cell present (Chvála, 1975; Grootaert & Chvála, 1992). The genus is distributed worldwide. Most species have been recorded from the Palaearctic realm, particularly from Europe where some 250 species are known (Chvála & Kovalev, 1989; Grootaert & Chvála, 1992). Smith (1975) reported 31 species from the Oriental Region. However since then, 28 species have been added to the fauna of China alone by Yang & Merz (2005), Yang, D. & Yang, C. (1989, 1990, 1992, 1997), Yang, C. & Yang, D. (1992), Saigusa & Yang (2002), and Yang, An & Gao (2002). So far 36 species are known to occur in China. The major reference dealing with *Platypalpus* are as following: Brunetti (1920), Frey (1943), Smith (1965), Chvála (1975, 1989), Grootaert (1984), and Grootaert & Chvála (1992).

Guangdong with a tropical or subtropical climate belongs to the South China Region of the Oriental realm north of Hongkong. The genus *Platypalpus* is here recorded for the first time from Guangdong. Three new species are described and illustrated. In addition two unnamed species, known from females alone, were found during the sampling campaign of Yang & Grootaert in 2003 in Guangdong. More species are expected to occur in this province since the sampling was done in the beginning of the flight period of *Platypalpus*. A key to the three described species from Guangdong is presented.

## MATERIAL AND METHODS

The specimens were collected at the end of May by Yang, Zhang & Grootaert respectively. The type material is deposited in the following collections:

CAU Entomological Museum of the China Agricultural University, Beijing, China

MHNG Muséum d'histoire naturelle, Genève, Switzerland

RBINS Royal Belgian Institute of Natural Sciences, Brussels, Belgium

In order to allow an easy comparison with descriptions of various authors, the morphological terminology follows generally Grootaert & Chvála (1992), except for crossveins which are written in capitals. Terminology of antenna follow Stuckenberg (1999).

The following abbreviations for bristles are used: acr-acrostichial, ad-anterodorsal, av-anteroventral, dc-dorsocentral, h-humeral, oc-ocellar, npl-notopleural, pd-posterodorsal, presc – prescutellar, psa-postalar, pv-posteroventral, sa-supraalar scutellar, vt-vertical.

## TAXONOMIC PART

### KEY TO THE DESCRIBED SPECIES OF *PLATYPALPUS* FROM GUANGDONG

The following key should help to separate quickly the three new species. Because of insufficient knowledge of the *Platypalpus* fauna of China a large number of additional species may be expected to occur in this province.

- |   |   |                              |
|---|---|------------------------------|
| 1 | Thorax black .....  | 2                            |
| - | Thorax yellow .....   | <i>guangdongensis</i> sp. n. |
| 2 | R <sub>4+5</sub> and M parallel apically; arista as long as postpedicel .....         | <i>zhangae</i> sp. n.        |
| - | R <sub>4+5</sub> and M convergent apically; arista much longer than postpedicel ..... | <i>convergens</i> sp. n.     |

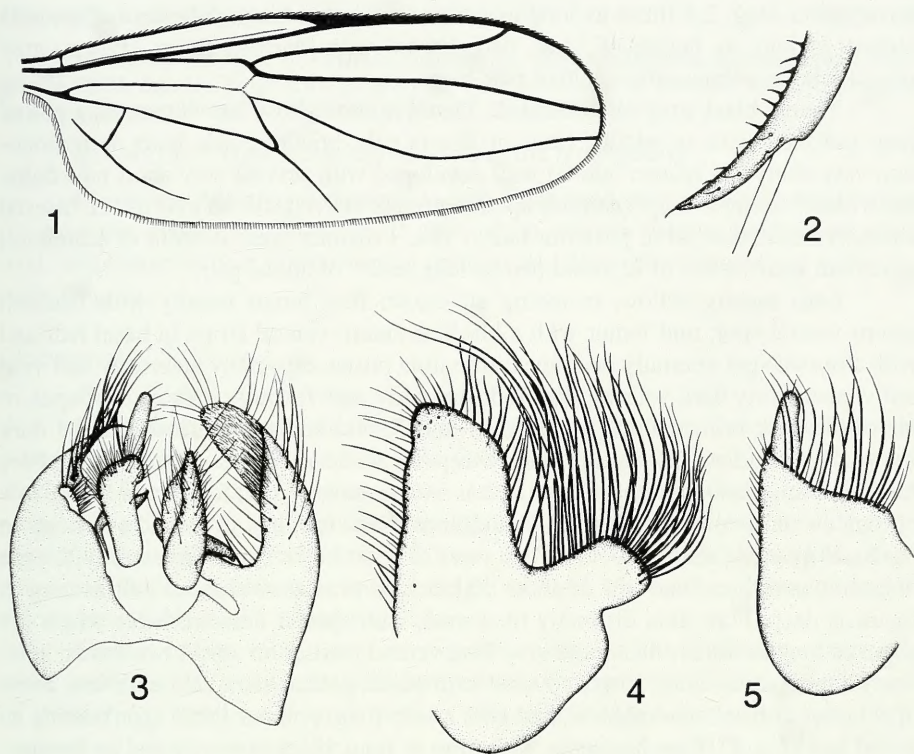
### *Platypalpus convergens* sp. n.

Figs 1-5

MATERIAL: Holotype ♂, CHINA: Guangdong: Ruyuan, Nanling National Nature Reserve, (23.20N/115.23E), Shumuyuan, 500 m, 26. III. 2003, leg. L. Zhang (CAU). Paratypes: 1 ♂ 12 ♀♀, same data as holotype (CAU & MNHG). 2 ♂♂, 7 ♀♀, forest near entrance of the Nanling National Nature Reserve, 26.III.2003, leg. P. Grootaert (sample 23008, RBINS). The type locality is a forest situated about 40 km north of Ruyuan (24.44N/113.18E).

ETYMOLOGY: The specific name refers to R<sub>4+5</sub> and M which are convergent apically.





FIGS 1-5

*Platypalpus convergens* sp. n, male. 1, wing; 2, tip of mid tibia; 3, genitalia, dorsal view; 4, left epiandrial lamella; 5, right epiandrial lamella.

**DIAGNOSIS:** Mainly grey-microtrichose species; postpedicel yellow, 2.8 times as long as wide, arista over twice as long; 1 pair of vt; hairs on mesonotum very short and sparse; mid femur with a row of rather short pv; fore tibia thickened with shorter dorsal and very long, dense black ventral bristles in apical half; mid tibia with very long apical spur (Fig. 2); fore basitarsus with long posterior and pv bristles;  $R_{4+5}$  and M convergent apically (Fig. 1).

#### DESCRIPTION:

*Male.* Body length 3.9-4.3 mm, wing length 4.8-4.9 mm.

Head black, grey microtrichose. Eyes narrowly separated on face; frons wider than face, parallel-sided, as wide as pedicel. Postocular hairs black above, very long and whitish below. Ocellar tubercle with 1 pair of short oc and 2 minute posterior hairs; 1 pair of short vt close together. Antenna with scape and basal half of pedicel dark brown, remainder yellow; arista dark brown; pedicel with a circle of black apical hairs; postpedicel long conical, 2.8 times as long as wide, with black hairs except base bare;

arista rather long, 2.6 times as long as postpedicel, short black pubescent. Proboscis almost as long as height of head, dark brown with blackish hairs; clypeus grey microtrichose; palpus yellow with 4 pale hairs.

Thorax black grey microtrichose. Pleura microtrichose but sternopleura with a large polished patch in middle. Hairs on thorax pale, bristles black; hairs on mesonotum very short and sparse; humeri well developed with several very short pale hairs, but without strong h; 1 npl (anterior npl absent), acr biserial, dc as long as acr, biserial anteriorly and uniserial in posterior half, 1 psa, 1 distinct presc in front of scutellum; scutellum with 2 pairs of sc, basal pair as long as 2/5 of apical pair.

Legs mainly yellow, including all coxae; fore femur basally with blackish antero-ventral spot; mid femur with a blackish antero-ventral stripe in basal half and with a brown spot ventrally near apex; fore tibia brown especially anteriorly and ventrally, posteriorly dark yellow. Mid tibia anteriorly and ventrally dark brown; apex of hind tibia dark brown; fore tarsomeres 1 and 5, mid and hind tarsomeres 3-5 dark brown. Hairs and bristles on legs black except for white av bristles on fore femur. Fore femur 1.8 times and mid femur 2.3 times as wide as hind femur; fore femur with a row of long av and a row of pv bristles (4 additional hairs forming an second outer row in the basal quarter); mid femur with two rows of short black spinules ventrally (longer in basal quarter) and one row of about 10 black pv bristles, which are half as long as femur is deep. Fore tibia distinctly thickened, with shorter dorsal bristles which are about as long as tibia is thick, and very long ventral bristles on apical two thirds; anteriorly almost along entire length covered with dense, golden hairs; mid tibia with a row of short weak black ventral hairs, and with a very long, pointed apical spur bearing an apical hair (Fig. 2). Fore basitarsus with rows of long, black posterior and pv bristles.

Wing hyaline; veins dark brown,  $R_{4+5}$  and M distinctly convergent apically (Fig. 1). Basal cells equally long. Anal vein distinct. Vein closing anal cell slightly S-shaped. Squama dark yellow with pale hairs. Halter yellow.

Abdomen subshining black, thinly grey microtrichose; hypopygium black. Hairs on abdomen short, pale. Male genitalia (Figs 3-5): Left epandrial lamella rather wide basally with distinct lateral process bearing very long marginal bristles; right epandrial lamella short with an apical row of long bristles, its apical projection (surstylus) short and finger-like; left cercus somewhat acute apically; right cercus short, obtuse apically.

*Female.* Body length 3.2-5.0 mm, wing length 4.4-4.5 mm. Similar to male, but legs almost entirely yellow without brown areas, fore tibia weakly thickened, without the very long black ventral hairs on tip, but being still longer haired than usual in *Platypalpus*.

DISTRIBUTION: China (Guangdong).

REMARKS: The new species is very peculiar. It is easily separated from other known species of the genus occurring in China by the fore tibia distinctly thickened with conspicuous dorsal and very long ventral bristles, and the long setulose fore basitarsus. *P. convergens* belongs to the *P. pallidiventris-cursitans* species-group of Chvála (1989).



*Platypalpus guangdongensis* sp. n.

Figs 6-9

**MATERIAL:** Holotype ♂, CHINA: Guangdong: Yingde, Shimentai National Forest Park, 28. III. 2003, leg. D. Yang (CAU). Paratype: 1 ♀, same data as holotype (CAU). The type locality is a forest situated 15 km north of Yingde (24.09N/113.25E).

**ETYMOLOGY:** The specific name refers to the type locality.

**DIAGNOSIS:** Mainly yellow species with black head, scutellum and mediotergite (postnotum); mesonotum subshiny; 2 pairs of vt; antenna yellow; postpedicel short oval; mid femur without posteroventral bristles; mid tibia with a long apical spur ventrally (Fig. 6).

**DESCRIPTION:**

*Male.* Body length 2.5 mm, wing length 4.0 mm.

Head black, grey microtrichose. Eyes narrowly separated on face; face narrower than frons. Hairs and bristles on head pale. Ocellar tubercle with 1 pair of oc and 4 very short posterior hairs; 2 vt. Antenna yellow; scape without dorsal bristles; pedicel with a circle of pale apical hairs; postpedicel short oval, 1.1 times as long as wide, with some apical hairs; arista very long, 3.9 times as long as postpedicel, blackish, short pubescent. Proboscis almost as long as height of head, brownish yellow with brown hairs; palpus yellow with 3 long pale hairs.

Thorax yellow, thinly grey microtrichose; mesonotum subshining; scutellum black, mediotergite (postnotum) blackish; polished spot on sternopleuron absent. Hairs on thorax pale, bristles brownish yellow; 1 short hair-like h curved inwards, 2 npl (anterior npl short and hair-like), acr 4-seriate, dc pale, as long as acr, 1 long psa, 1 short weak presc in front of scutellum, scutellum with 2 pairs of sc (basal pair very short, one third as long as apical pair).

Legs yellow, but tarsomere 5 of all legs brown. Hairs on legs pale. Fore femur 1.2 times and mid femur 1.8 times as wide as hind femur; mid femur with two rows of short black ventral spinules (av very short, pv slightly longer than av bristles, but ventral bristles on basal 1/4 long and brownish yellow), without row of strong pv bristles; mid tibia with a row of blackish ventral bristles and finger-like apical spur (Fig. 6).

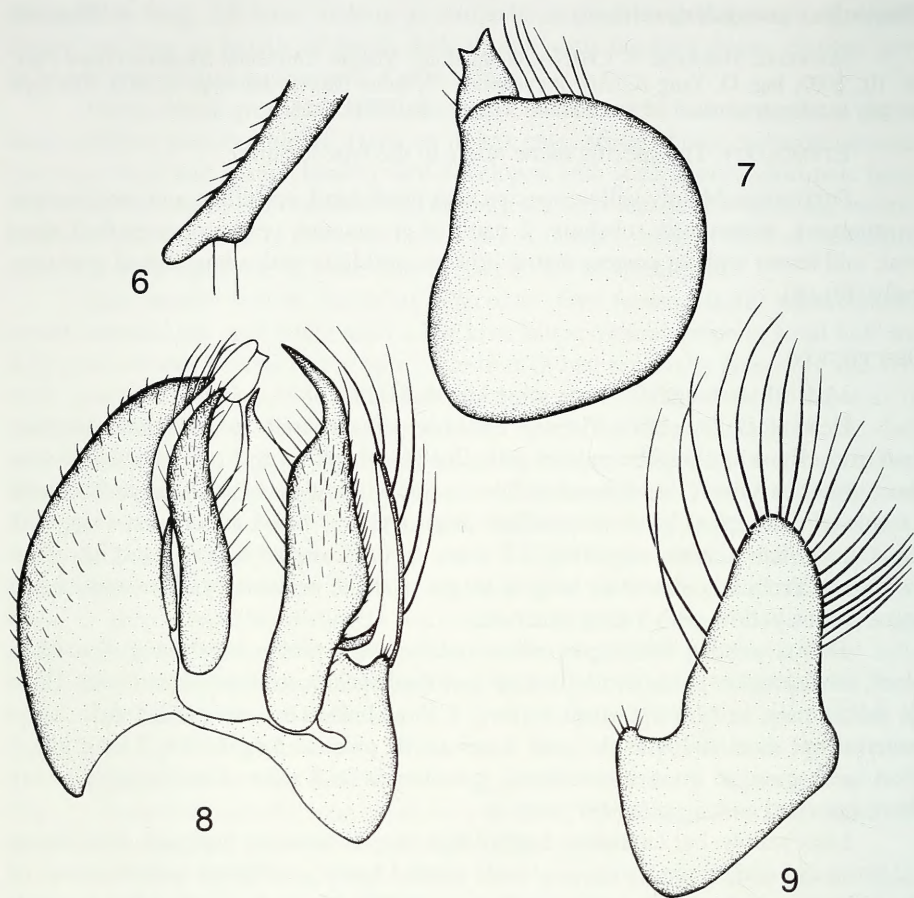
Wing hyaline; veins brownish yellow,  $R_{4+5}$  and M parallel apically. Basal cells equal, crossveins contiguous. Squama yellow with pale hairs. Halter yellow.

Abdomen brownish yellow, pale grey microtrichose; sternites dark yellow, hypopygium brownish. Hairs on abdomen pale. Male genitalia (Figs 7-9): Left epandrial lamella rather narrow in dorsal view, its apical projection (surstylus) large and subtriangular with long apical bristles; right epandrial lamella slightly widening dorsally, its apical projection (surstylus) rather small truncate apically; left cercus rather long, spine-like apically; right cercus short with acute apex.

*Female.* Body length 2.0 mm, wing length 2.8 mm. Similar to male, but abdomen entirely dark yellow.

**DISTRIBUTION:** China (Guangdong).

**REMARKS:** The new species is very similar to *Platypalpus guangxiensis* Yang & Yang from Guangxi, Sichuan and Hubei, but can be separated from the latter by the



FIGS 6-9

*Platypalpus guangdongensis* sp. n, male. 6, tip of mid tibia; 7, right epandrial lamella; 8, genitalia, dorsal view; 9, left epandrial lamella.

blackish mediotergite and short thick apical projection of the right epandrial lamella. In *P. guangxiensis*, the mediotergite is yellow, and the apical projection of the right epandrial lamella is long and spine-like (Yang & Yang, 1992). The unusual combination of characters does not allow to place this species in one of the species-groups defined by Chvála (1989).

***Platypalpus zhangae* sp. n.**

Figs 10-13

**MATERIAL:** Holotype ♂, CHINA: Guangdong: Ruyuan, Nanling National Nature Reserve, (23.20N/115.23E), Shumuyuan, 500 m, 26. III. 2003, leg. Lili Zhang (CAU). Paratype: 1 ♂. Guangdong, Ruyuan, forest near entrance of the Nanling National Nature Reserve, 26.III.2003, leg. P. Grootaert (sample 23008, RBINS). The type locality is a forest situated about 40 km north of Ruyuan (24.44N/113.18E).



ETYMOLOGY: The species is named after the collector of the holotype.

DIAGNOSIS: Mainly black species with shining black mesonotum; 1 pair of vt; postpedicel much elongated, 3.8 times longer than wide; arista rather short, at most as long as postpedicel (Fig. 10); costa with a black stigma; mid femur without pv bristles; mid tibia black without apical spur.

DESCRIPTION:

*Male.* Body length 3.0 mm, wing length 3.2 mm.

Head black, grey microtrichose. Eyes narrowly separated on face; frons wider than face. Hairs on head pale, bristles brownish yellow. Ocellar tubercle with 1 pair of oc and 4 posterior hairs slightly shorter than oc; 1 pair of short vt. Antenna (Fig. 10) blackish with black scape; pedicel with a circle of black apical hairs; postpedicel long conical, 3.8 times longer than wide, with blackish hairs except base bare; arista rather short, as long as postpedicel, blackish, short pubescent. Proboscis almost as long as height of head, dark brown with blackish hairs; palpus rather large, ovoid, yellow with 3 minute blackish hairs.

Thorax black, but humeri and prothorax paler (at least in alcohol preserved specimens); mesonotum polished, sparsely haired but laterally with dense hairs; pleuron subshiny, polished spot on sternopleuron not discernible. Hairs on thorax pale, bristles brownish yellow; humerus with 6 hairs including 1 rather long hair-like h curved inward; 1 npl (anterior npl absent), acr rather long, biseriate, diverging, dc uniseriate and shorter than acr, 1 psa, 1 short presc in front of scutellum; scutellum very short densely pubescent, with 2 pairs of sc, basal pair 2/3 as long as apical pair.

Legs dark brownish yellow; all coxae and trochanters yellow; mid tibia black, hind tibia dark brown; tarsomere 5 dark brown. Hairs and bristles on legs pale. Fore femur 1.2 times and mid femur 1.4 times as wide as hind femur; fore femur with a row of av and a row of short pv bristles, which are as long as femur is wide; mid femur with two rows of black ventral spinules (av short and pv rather long), but without row of strong pv bristles; mid tibia with a row of short black ventral bristles, and without apical spur.

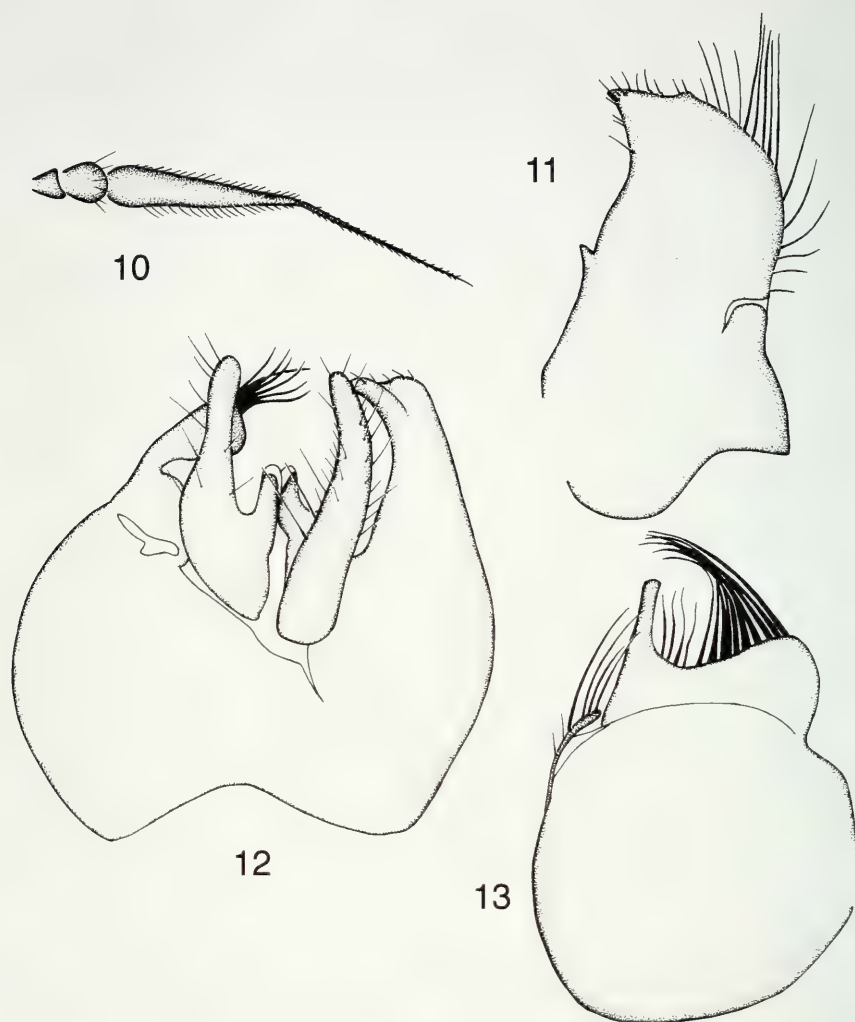
Wing nearly hyaline; veins dark brown, C with a black stigma;  $R_{4+5}$  and M parallel apically. Basal cells equally long. Vein closing anal cell recurrent (brown on basal half, tip indistinct). Anal vein weakly indicated. Anal lobe of wing narrow. Squama yellow with pale hairs. Halter pale yellow.

Abdomen blackish, grey microtrichose; hypopygium black. Hairs on abdomen pale, dense, long at sides. Male genitalia (Figs 11-13): Left and right epandrial lamellae rather broadly fused basally (best seen in dorsal view); left epandrial lamella rather narrow in dorsal view, its apical projection (surstylus) rather large and not distinctly separated from basal plate; right epandrial lamella rather wide in dorsal view, its apical projection (surstylus) short and wide with a finger-like apico-lateral process; left and right cerci basally with a medial process and apically finger-like.

*Female.* Unknown.

DISTRIBUTION: China (Guangdong).

REMARKS: The new species is somewhat similar to *Platypalpus pallipilosus* Saigusa & Yang from Henan, but can be separated from the latter by the long post-



FIGS 10-13

*Platypalpus zhangae* sp. n. male. 10, antenna; 11, left epandrial lamella; 12, genitalia, dorsal view; 13, right epandrial lamella.

pedicel (3.8 times longer than wide) with the rather short arista (as long as the postpedicel). In *P. pallipilosus*, the postpedicel is shorter (2.1 times longer than wide) with a longer arista (1.9 times longer than the postpedicel). Judging from the wing structure, the shining mesonotum, the rather thin mid femur and the long antenna *P. zhangae* belongs to the *P. longicornis* species-group. However, instead of two pairs of vertical bristles usually present in this species-group there is only one pair developed in the new species.



## CONCLUSIONS

Guangdong belongs to the South China region of the Oriental realm with a sub-tropical and tropical climate. *Platypalpus* is apparently a more temperate genus which is less well represented in hot, tropical parts of the world. Therefore it is not surprising that up to now only 5 species of *Platypalpus* are known to occur in Guangdong, three of which are described in this paper and two remain unnamed. Nevertheless, taking into account the insufficient collecting effort, the rather early collecting time and the difficulties to find suitable habitats, it is highly possible that more species will eventually be found in this province of China.

## ACKNOWLEDGEMENTS

Our sincere thanks are due to Mrs Lili Zhang and Mrs Mengqing Wang (China Agricultural University, Beijing) for their help during the study. The research was funded by the National Natural Science Foundation of China (No. 30070100\_No. 30225009).

## REFERENCES

- BRUNETTI, E. 1920. Diptera Brachycera Vol. 1. *The Fauna of British India, including Ceylon & Burma*. London, 401 pp.
- CHVÁLA, M. 1975. The Tachydromiinae (Dipt. Empididae) of Fennoscandia and Denmark. I. *Fauna Entomologica Scandinavica* 3: 1-336. Scandinavian Science Press, Copenhagen.
- CHVÁLA, M. 1989. Monograph of northern and central European species of *Platypalpus* (Diptera, Hybotidae), with data on the occurrence in Czechoslovakia. *Acta Universitatis Carolinae - Biologica* 32: 209-376.
- CHVÁLA, M. & KOVALEV, V. G. 1989. Family Hybotidae (pp. 174-227). In: Soós, Á. & PAPP, L. (eds). Catalogue of Palaearctic Diptera. Vol. 6. *Akadémiai Kiadó, Budapest*, 435 pp.
- FREY, R. 1943. Übersicht der paläarktischen Arten der Gattung *Platypalpus* Macq. (= *Coryneta* Meig.). (Dipt., Empididae). *Notulae Entomologicae* 23: 1-19.
- GROOTAERT, P. 1984. Two new species of *Platypalpus* Macquart (Diptera, Empidoidea, Hybotidae) from Papua New Guinea. *Bulletin et Annales de la Société Royale d'Entomologie de Belgique* 120: 283-290.
- GROOTAERT, P. & CHVÁLA, M. 1992. Monograph of the genus *Platypalpus* (Diptera: Empidoidea, Hybotidae) of the Mediterranean region and the Canary Islands. *Acta Universitatis Carolinae - Biologica* 36: 3-226.
- SAIGUSA, T. & YANG, D. 2002. Empididae (Diptera) from Funiu Mountains, Henan, China (I). *Studia Dipterologica* 9 (2): 519-543.
- SMITH, K. G. V. 1965. Diptera from Nepal: Empididae. *Bulletin of the British Museum (Natural History), Entomology* 17 (2): 61-112.
- SMITH, K. G. V. 1975. Family Empididae (pp. 185-211). In: DELFINADO, M. D. & HARDY, D. E. (eds). A Catalog of the Diptera of the Oriental Region. Vol. 2. *The University Press of Hawaii, Honolulu*, 459 pp.
- STUCKENBERG, B. R. 1999. Antennal evolution in the Brachycera (Diptera), with a reassessment of terminology relating to the flagellum. *Studia Dipterologica* 6 (1): 33-48.
- YANG, C. & YANG, D. 1992. Three new species of Empididae from Guangxi – Diptera: Brachycera. *Journal of the Guangxi Academy of Sciences* 8 (1): 44-48.
- YANG, D., AN, S. & GAO, C. 2002. New species of Empididae from Henan (Diptera) (pp. 30-38). In: SHEN, X. & SHI, Z. (eds). The Fauna and Taxonomy of Insects in Henan. Vol. 5. *China Agricultural Sciencetech Press, Beijing*, 453 pp.

- YANG, D. & MERZ, B. (2005). Review of the species of *Platypalpus* Macquart from Guangxi, China (Diptera, Hybotidae, Tachydromiinae). *Revue suisse de zoologie* 112(4): 849-857.
- YANG, D. & YANG, C. 1989. The dance flies of Xizang (II) (Diptera: Empididae). *Acta Agriculturae Universitatis Pekinensis* 15 (4): 415-424.
- YANG, D. & YANG, C. 1990. Eleven new species of the subfamily Tachydrominae from Yunnan (Diptera: Empididae). *Zoological Research* 11 (1): 63-72.
- YANG, D. & YANG, C. 1992. Diptera: Empididae (pp. 1089-1097). In: CHEN, S. (ed.). Insects of the Hengduan Mountains Region. Vol. 2. *Science Press, Beijing*, 1547 pp.
- YANG, D. & YANG, C. 1997. Diptera: Empididae (pp. 1469-1476). In: YANG, X. (ed.). Insects of the Three Gorge Reservoir Area of Yangtze River. *Chongqing Publishing House, Chongqing*, 1847 pp.



## New species and records of the genus *Basanus* Lacordaire (Insecta: Coleoptera: Tenebrionidae)\*

Wolfgang SCHAWALLER

Staatliches Museum für Naturkunde, Rosenstein 1, D-70191 Stuttgart, Germany.

E-mail: schawaller.smns@naturkundemuseum-bw.de

**New species and records of the genus *Basanus* Lacordaire (Insecta: Coleoptera: Tenebrionidae).** - Newly collected specimens of the genus *Basanus* Lacordaire, 1859 from southeastern Asia are presented, including new distributional data and new species: *Basanus halmahericus* sp. n. (Moluccas: Halmahera), *Basanus luzonicus* sp. n. (Philippines: Luzon), *Basanus poringicus* sp. n. (Borneo: Sabah). For *Basanus philippinensis* Gebien, 1925 lectotype and paralectotypes are designated.

**Keywords:** Tenebrionidae - *Basanus* - new species - distribution - figures.

### INTRODUCTION

The genus *Basanus* Lacordaire, 1859 was revised by Gebien (1925), a few further species were described by Schawaller (1995) and by Masumoto & Merkl (2003). The congeners are distributed in the Palaearctic Far East (including the Ussuri Region, Korea, Japan and Taiwan), continental southeastern Asia, the Himalayas, the Philippines, the Sunda Islands, Moluccas and New Guinea. In this contribution, accumulated specimens from different collections are presented, including new taxa and new distributional data. Two additional new species are available but are not described because of the lack of males.

The generic and specific characters of *Basanus* have been discussed by Schawaller (1995). Unfortunately, the shape of the aedeagus within this genus is relatively simple and not distinctly modified between the species (compare Figs 1-5). The generic limits of *Basanus* Lacordaire, 1859, *Spiloscapa* Bates, 1873 and *Scaphidema* Redtenbacher, 1849 are still unclear. Doyen *et al.* (1989) listed some adult and larval synapomorphic characters and included *Basanus* in the subtribe Scaphidemini within the tribe Diaperini.

### ACRONYMS OF DEPOSITORIES

CHBM	Collection Prof. Dr Hans Bremer, Zoologische Staatssammlung, München
CRGT	Collection Dr Roland Grimm, Tübingen
CSBC	Collection Stanislav Bečvář, České Budějovice
HNHM	Hungarian Natural History Museum, Budapest (Dr Ottó Merkl)
MHNG	Muséum d'histoire naturelle, Genève (Dr Giulio Cuccodoro)
NHMB	Naturhistorisches Museum, Basel (Dr Michel Brancucci)
NHMB-F	Naturhistorisches Museum, Basel, collection G. Frey (Dr Eva Sprecher)
SMNS	Staatliches Museum für Naturkunde, Stuttgart (author)
SMTD	Staatliches Museum für Tierkunde, Dresden (Olaf Jäger)

\* Contributions to Tenebrionidae, no. 55. - For no. 54 see Zootaxa, special issue Martens, 2006.  
Manuscript accepted 17.11.2005

## THE SPECIES STUDIED

***Basanus amamianus* Chujo, 1966**

Fig. 6

MATERIAL: Japan, Ryukyu Islands, Okinawa, Yona, Kunigami, 18.-20.III.1991, leg. T. Ueno, 1 ex. SMNS.

DISTRIBUTION: Japan, Ryukyu Islands (type locality).

***Basanus erotyloides* Lewis, 1891**

MATERIAL: China, Shaanxi Prov., Taibai Shan above Houzhenzi, 1300-1700 m, 9.VI.-3.VII.1998, leg. J. Martens & P. Jäger, 1 ex. SMNS. – Japan, Ehime Pref., Mt. Takanawasan, 7.V.1997, leg. H. Kan, 2 ex. SMNS. – Japan, Kyushu, Ohita Pref., Yoshibu, 19.VIII.1995, leg. T. Ueno, 2 ex. SMNS. – Annam, Phuc-Son, holotype of syn. *annamitus* Gebien, 1925, SMTD.

DISTRIBUTION: Japan (type locality), China, Indochina.

***Basanus fruhstorferi* Gebien, 1940**

Fig. 7

MATERIAL: S Celebes (Sulawesi), Lompa-Battau, 3000 ft., III.1896, leg. H. Fruhstorfer, holotype NHMB-F (labelled as type), 1 paratype SMTD (labelled as cotype).

DISTRIBUTION: Sulawesi (type locality).

***Basanus halmahericus* sp. n.**

Figs 1, 8

HOLOTYPE (♂): Moluccas (=Maluku), Halmahera, Sidangoli, Batu Putih, 100 m, 23.XI.1999, leg. A. Riedel, SMNS.

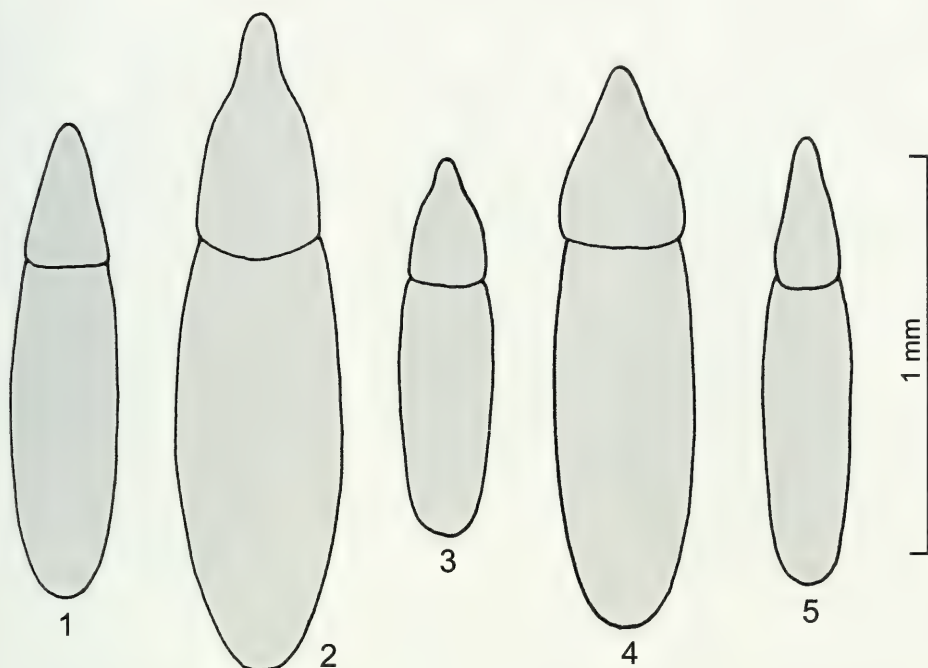
PARATYPES: Moluccas, Halmahera, Ibu, Desa Nanas, Gunung (= Mt.) Gamkonora, 100-1000 m, 27.XI.1999, leg. A. Riedel, 2 ex. SMNS. – Moluccas, Halmahera, Buli, Maba, 20-200 m, 6.-7.XI.1999, leg. A. Riedel, 1 ex. SMNS.

ETYMOLOGY: Named after the island Halmahera where the type series was collected.

DESCRIPTION: Shape and colour pattern of pronotum and elytra see Fig. 8. Head, pronotum and scutellum black with greenish metallic shine; elytron with identical metallic shine and with a bigger round yellow spot before the middle and a smaller yellow round spot before the tip; antenna completely black, legs light ferrugineous with darker tibiae; ventral side black, ventrites red ferrugineous. Head with denser and coarser punctation than on pronotum. Pronotum with distinct punctures, distance of the punctures 4-8 times longer than the diameter; anterior margin completely bordered, basal margin unbordered. Elytron with 8 rows of punctures, rows indistinct in the anterior part, third row with about 25 punctures; intervals flat, with scattered punctures; lateral margin to be seen nearly on its total length. Aedeagus see Fig. 1. Body length 7.2-8.0 mm.

DIAGNOSIS: To be recognized by the metallic dorsal side with small and round elytral spots and by the shape of the aedeagus. A similar colour pattern and also a metallic surface possess *Basanus hellus* Gebien, 1925 from the Philippines, but this species is distinctly smaller (body length 4.2 mm) and the body is highly convex, so that the lateral margin of the elytra can be seen in dorsal view only near the shoulders, whereas in *Basanus halmahericus* sp. n. the lateral margin can be seen nearly on its total length.





FIGS 1-5

Aedeagus of *Basanus* species in dorsal view. 1: *B. halmahericus* sp. n., holotype, SMNS. 2: *B. javanus*, aberrant non-type, W Malaysia, CSBC. 3: *B. luzonicus* sp. n., holotype, SMNS. 4: *B. philippinensis*, lectotype, NHMB-F. 5: *B. poringicus* sp. n., holotype, MHNG.

***Basanus javanus* Chevrolat, 1878**

Figs 2, 9

**MATERIAL:** S Sulawesi, Tanah Toraja, Pulu Pulu, 1700 m, 13.-16.VIII.1990, leg. A. Riedel, 5 ex. SMNS. – Sulawesi, Kotamobagu, Modoinding, Gunung (= Mt.) Ambang, 1100-1450 m, 6.XII.1999, leg. A. Riedel, 1 ex. SMNS. – SE Burma, 5.XI.1989, leg. S. Stahnke, 1 ex. SMNS. – NE Laos, Hua Phan Prov., Ban Saluei, Phu Phan Mt, 1500-2000 m, 26.IV.-11.V.2001, leg. J. Bezdek, 2 ex. SMNS. – W Malaysia, Island Tioman, Kampong Tekek, 9.III.1998, leg. L. Dembický & P. Pacholátka, 1 ex. NHMB. – W Malaysia, Perak, Maxwell Hill above Taiping, 900-1000 m, 12.-16.I.1995, leg. S. Bečvář, 1 ex. CSBC. – N Thailand, W Chiang Mai, Doi Suthep Pui NP, 30.V.1999, leg. R. Grimm, 1 ex. CRGT.

**REMARKS:** The single male from W Malaysia/Maxwell Hill possesses a somewhat different colour pattern with the anterior elytral spots round (Fig. 9) and not banded (Schawaller 1995: fig. 5) as usually present in this species. The other diagnostic characters (thick antennae, ventral side black, shape of the aedeagus: Fig. 2) coincide.

**DISTRIBUTION:** Java (type locality), Borneo, Sulawesi (new record), Myanmar, Laos, Vietnam, W Malaysia (new record), Thailand (new record).

***Basanus longior* Gebien, 1925**

Fig. 10

**MATERIAL:** Sumatra, 1 ex. NHMB-F. – W Sumatra, Payakumbuh, Harau Valley, 9.-29.X.1991, leg. A. Riedel, 1 ex. SMNS. – Borneo, Sabah, Mt. Kinabalu NP, Poring Hot Springs, 520 m, 13.V.1987, leg. A. Smetana, 1 ex. SMNS (duplicate from MHNG).

REMARKS: The pronotum varies from completely black up to black with lighter margins.

DISTRIBUTION: Sumatra (type locality), Borneo (new record).

***Basanus luzonicus* sp. n.**

Figs 3, 11

HOLOTYPE (♂): Philippines, N Luzon, Mountain Prov., Bontoc Region, NW Barlig, 2000 m, 9.IV.2000, leg. L. Dembický, SMNS.

PARATYPES: Philippines, Luzon, Mt. Polis, leg. Boettcher, 12 ex. SMTD, 2 ex. SMNS, 2 ex. NHMB-F.

ETYMOLOGY: Named after the Philippine Island Luzon, where the type series was collected.

DESCRIPTION: Shape and colour pattern of pronotum and elytra see Fig. 11. Head, pronotum and scutellum dark ferrugineous without metallic shine, lateral margin of pronotum somewhat lighter; elytron also dark ferrugineous and with a bigger round yellow spot before the middle and a smaller yellow round spot before the tip; antenna completely dark ferrugineous with the tip of the last antennomere somewhat lighter, legs ferrugineous; ventral side including ventrites dark ferrugineous. Head with denser and coarser punctation than on pronotum. Pronotum with distinct punctures, distance of the punctures 4-8 times longer than the diameter; anterior margin completely bordered, basal margin unbordered. Elytron with 8 rows of punctures, rows indistinct in the anterior part, third row with about 30 punctures; intervals flat, with scattered punctures; lateral margin to be seen in dorsal view nearly on its total length. Aedeagus see Fig. 3. Body length 5.2-6.2 mm.

DIAGNOSIS: To be recognized by the smaller body size, by the elytral colour pattern, by the indistinct elytral rows and by the shape of the aedeagus. *Basanus luzonicus* sp. n. is quite similar to *Basanus philippinensis* Gebien, 1925 also from the Philippines, but in this species the elytral colour pattern is different (anterior spot transverse, band-like and with sutural interruption, Fig. 12), the punctural rows on the elytra are dense and distinct and the aedeagus is slightly different (compare Figs 3-4).

REMARKS: This species-group includes also 2 additional new species from Borneo and Sumatra, which are listed below, but which are not described because of the lack of males. Both have a similar dorsal colour pattern (Figs 16-17) as in *Basanus luzonicus* sp. n. (Fig. 11), but a different dorsal punctation and a different structure of the elytral intervals.

***Basanus philippinensis* Gebien, 1925**

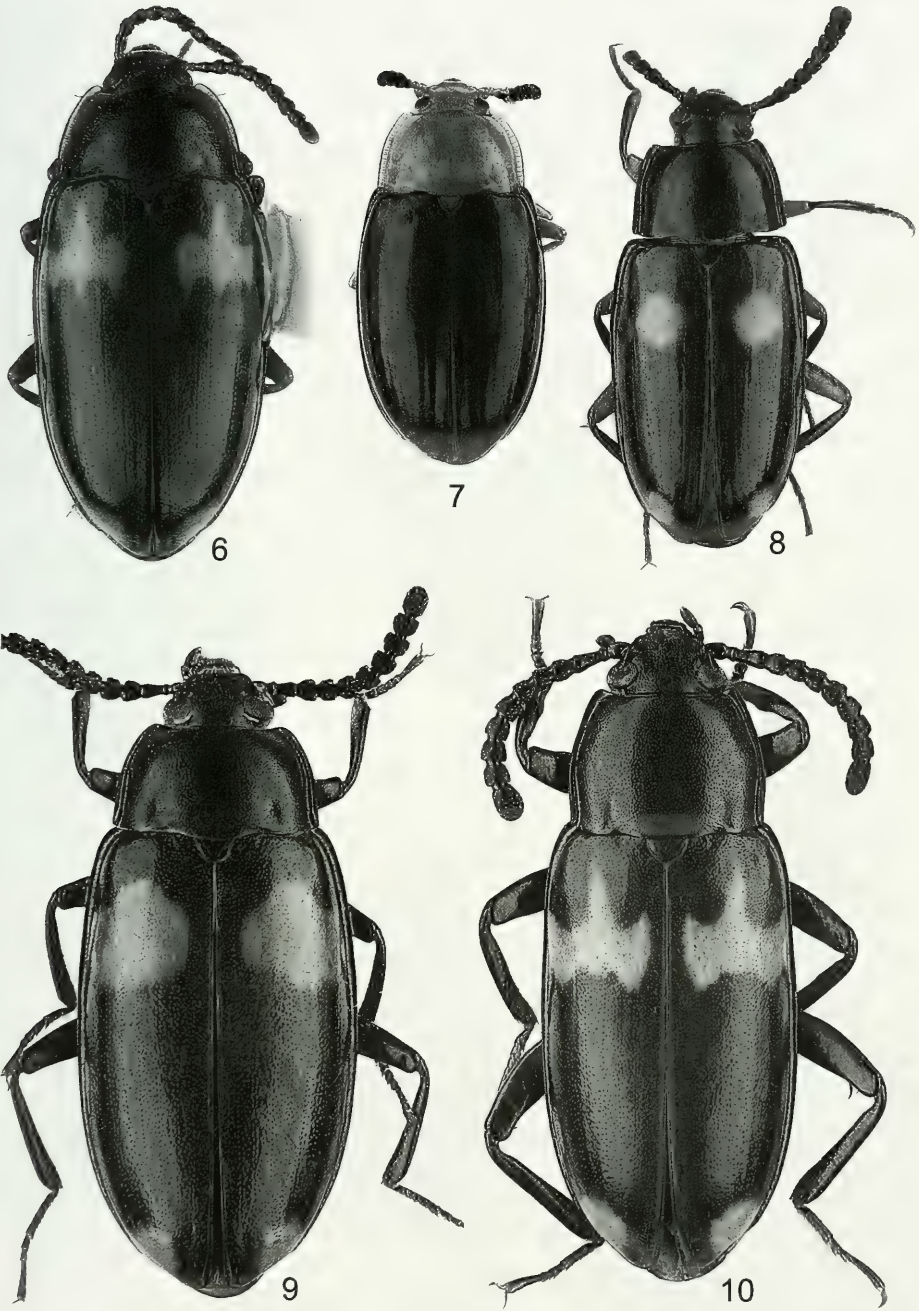
Figs 4, 12

MATERIAL: Philippines, leg. Semper, 1 ♂ cotype NHMB-F, designated herewith as lectotype. – Philippines, Luzon, Malinao, Tayabas, leg. Baker, 1 ♀ cotype NHMB-F, 1 cotype SMTD, both designated herewith as paralectotypes. – Philippines, Luzon, Mt. Makiling, leg. Baker, 1 cotype SMTD, designated herewith as paralectotype.

REMARKS: The lectotype and paralectotypes are designated in order to preserve stability of the nomenclature in this group, according to the Article 74.7.3 of the International Code of Zoological Nomenclature (1999).

DISTRIBUTION: Philippines (type localities).





FIGS 6-10

Dorsal view of *Basanus* species. 6: *B. amamianus*, non-type, Okinawa, SMNS. 7: *B. fruhstorferi*, paratype, SMTD. 8: *B. halmahericus* sp. n., holotype, SMNS. 9: *B. javanus*, aberrant non-type, W Malaysia, CSBC. 10: *B. longior*, non-type, Sumatra, SMNS.

***Basanus poringicus* sp. n.**

Figs 5, 13

HOLOTYPE (♂): Borneo, Sabah, Mt. Kinabalu NP, Poring Hot Springs, 500 m, 8.V.1987, leg. D. Burckhardt & I. Löbl, MHNG.

PARATYPE: Same data as holotype, 1 ex. SMNS.

ETYMOLOGY: Named after the type locality Poring.

DESCRIPTION: Shape and colour pattern of pronotum and elytra see Fig. 13. Head red ferrugineous, pronotum red ferrugineous with 2 darker longitudinal spots, scutellum red ferrugineous; elytron darker ferrugineous and with a large, yellow spot in the anterior part; antenna dark ferrugineous with the 3 basal segments somewhat lighter and coloured like the head, legs completely ferrugineous; ventral side including ventrites red ferrugineous. Head with denser and coarser punctation than on pronotum. Pronotum with distinct punctures, distance of the punctures 2-5 times longer than the diameter, additionally with scattered and distinctly bigger punctures; anterior margin completely bordered, basal margin unbordered. Elytron with 8 rows of punctures, third row with about 50 punctures; intervals convex, with a few scattered punctures; lateral margin to be seen nearly on its total length. Aedeagus see Fig. 5. Body length 5.8-6.0 mm.

DIAGNOSIS: *Basanus poringicus* sp. n. can be recognized by the dorsal colour pattern (Fig. 13), by convex elytral intervals and by the shape of the aedeagus. The colour pattern combined with convex elytral intervals are quite unusual within the genus and do not occur in any other congeners.

***Basanus soppongensis* Schawaller, 1995**

MATERIAL: Vietnam, Nam Cat NP, 4.-11.V.1994, leg. J. Zacharda, 1 ex. CHBM.

DISTRIBUTION: Thailand (type locality), Vietnam (new record).

***Basanus sulawesicus* (Schawaller, 1997)**

Fig. 14

MATERIAL: C Sulawesi, Palu, Palolo, Lindu NP, 25.-27.VIII.1990, leg. A. Riedel, ♂ holotype SMNS.

REMARKS: Transferred from the genus *Spiloscapa* Bates, 1873 to the genus *Basanus* Lacordaire, 1859 by Schawaller (2004).

DISTRIBUTION: Sulawesi (type locality).

***Basanus sumatranus* Gebien, 1925**

Fig. 15

MATERIAL: Sumatra, Solok, ♀ holotype NHMB-F (labelled as type)

REMARKS: Gebien (1925) named this species for the first time in the key on page 145 *sumatrensis* and later in the description on page 147 and in the legend of the plate *sumatranus*, the type specimen is also labelled as *sumatranus*. Thus, *sumatrensis* in the key is obviously a printing error and I fix here the name *sumatranus* for this species.

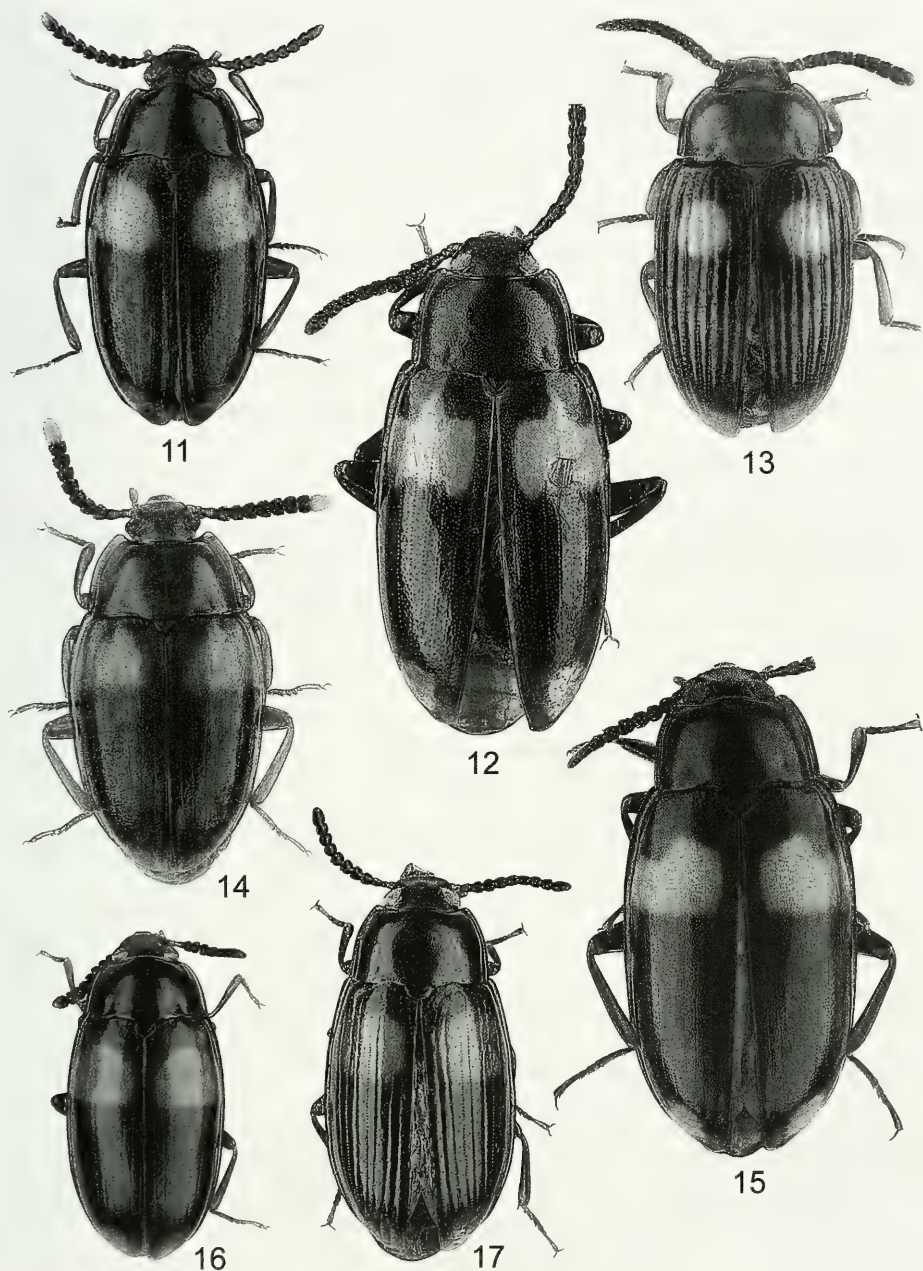
DISTRIBUTION: Sumatra (type locality).

***Basanus* sp. A ♀**

Fig. 16

MATERIAL: Borneo, Sabah, Mt. Kinabalu NP, Headquarters, 1560 m, 3.-13.VIII.1988, leg. A. Smetana, 1 ♀ MHNG.





FIGS 11-17

Dorsal view of *Basanus* species. 11: *B. luzonicus* sp. n., holotype, SMNS. 12: *B. philippinensis*, lectotype, NHMB-F. 13: *B. poringicus* sp. n., holotype, MHNG. 14: *B. sulawesicus*, holotype, SMNS. 15: *B. sumatranus*, holotype, NHMB-F. 16: *Basanus* sp. A, ♀, Borneo, MHNG. 17: *Basanus* sp. B, ♀, Sumatra, SMNS.

REMARKS: To be recognized by the small body size (5.0 mm), by the dorsal colour pattern (Fig. 16), by the ferrugineous ventral side, and by a fine but dense punctation on the elytra without distinct punctural rows and with absolutely flat intervals. The specimen presents a new species, but I avoid to describe it because of the lack of males.

***Basanus* sp. B ♀**

Fig. 17

MATERIAL: Sumatra, Bengkulu, 20 km S Muko Muko, 20 m, 16.VIII.1981, leg. D. Erber, 1 ♀ SMNS.

REMARKS: To be recognized by the small body size (5.5 mm), by the dorsal colour pattern (Fig. 17), by the ferrugineous ventral side, and by distinct punctural rows on the elytra with slightly convex intervals. The specimen presents a further new species, but I also avoid to describe it because of the lack of males.

### ACKNOWLEDGEMENTS

Thanks are due to all colleagues and friends loaning material from their collections, they are compiled in the list of the depositories. The hospitality of Dr Ottó Merkl (Budapest) and Dr Eva Sprecher (Basel) during my visits is greatly appreciated. Johannes Reibnitz (Stuttgart) kindly prepared again the photographs and arranged them on plates.

### REFERENCES

- DOYEN, J. T., MATTHEWS, E. G. & LAWRENCE, J. F. 1989. Classification and annotated checklist of the Australian genera of Tenebrionidae (Coleoptera). *Invertebrate Taxonomy* 3: 229-260.
- GEBIEN, H. 1925. Die Tenebrioniden (Coleoptera) des Indo-Malayischen Gebietes, unter Berücksichtigung der benachbarten Faunen, IV. Die Gattungen *Phloeopsidius*, *Dysantes*, *Basanus*, und *Diaperis*. *Philippine Journal of Science* 27: 131-157.
- ICZN, 1999. *International Code of Zoological Nomenclature*, 4th Edition. xxix + 306 pp. International Trust for Zoological Nomenclature, c/o The Natural History Museum, London.
- MASUMOTO, K. & MERKL, O. 2003. A new *Spiloscapa* and a new *Basanus* from Taiwan (Coleoptera. Tenebrionidae. Scaphidemini). *Entomological Review of Japan* 58: 165-171.
- SCHAWALLER, W. 1995. The genus *Basanus* Lacordaire (Coleoptera. Tenebrionidae) in continental south-eastern Asia. *Acta Zoologica Academiae Scientiarum Hungaricae* 41: 327-334.
- SCHAWALLER, W. 2004. New species and records of the genus *Spiloscapa* Bates (Coleoptera. Tenebrionidae) from the Oriental and Papuan Regions. *Stuttgarter Beiträge zur Naturkunde* (A) 661: 1-10.

**Further considerations regarding the status of *Grosphus madagascariensis* (Gervais) and *Grosphus hirtus* Kraepelin, and description of a new species (Scorpiones, Buthidae)**

Wilson R. LOURENÇO<sup>1</sup> & Steven M. GOODMAN<sup>2</sup>

<sup>1</sup>Département de Systématique et Evolution, USM 0602, Section Arthropodes (Arachnologie), Muséum national d'Histoire naturelle, CP 053, 61 rue Buffon, 75005 Paris, France. E-mail: arachne@mnhn.fr

<sup>2</sup>Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605, USA, and WWF, BP 738, Antananarivo (101), Madagascar. E-mail: sgoodman@fieldmuseum.org

**Further considerations regarding the status of *Grosphus madagascariensis* (Gervais) and *Grosphus hirtus* Kraepelin, and description of a new species (Scorpiones, Buthidae).** - New considerations regarding the species *Grosphus madagascariensis* (Gervais, 1843), type species of the genus *Grosphus* Simon, 1880, and *Grosphus hirtus* Kraepelin, 1900 are proposed, and both species are redescribed. One new species, *Grosphus goudoti* sp. n., is described from the Province d'Antsiranana, Forêt de Bobankora, E of Daraina on the northern range of Madagascar. With this description the total number of known species in this endemic genus is now 15. Some details are presented on the ecological settings of the sites where the described specimens were collected. A revised key to the species of *Grosphus* is given.

**Keywords:** Scorpiones - Buthidae - *Grosphus* - new species - taxonomy - Madagascar.

## INTRODUCTION

As already discussed in recent papers (Lourenço, 2003; Lourenço *et al.*, 2004), the first *Grosphus* species to be described was *Scorpio* (*Androctonus*) *madagascariensis* Gervais, 1843 = *G. madagascariensis* (Gervais, 1843). Kraepelin (1900) contributed to the study of this genus and described several new species, including *G. hirtus*, a species morphologically similar to *G. madagascariensis*. In his monograph on the scorpions of Madagascar, Fage (1929) characterized both species. After Fage's (1929) monograph several new species of *Grosphus* were described (e. g. Lourenço, 2003; Lourenço *et al.*, 2004), and precise diagnoses have been proposed for *G. madagascariensis* and *G. hirtus* (see Lourenço, 1996).

The taxonomy of *Grosphus* is based mainly on two characters: the pattern of coloration and the morphology of the basal middle lamellae of the female pectines.



This last character has been considered by scorpion taxonomists to be of species specific significance and possess little intraspecific variation. However, more detailed investigations have showed that in some cases closely related species have a similar basal middle lamellae morphology (Loureço, 2003; Loureço & Goodman, 2003; Loureço *et al.*, 2004). On the basis of this character some populations which have been attributed to widely distributed species, such as *G. madagascariensis*, *G. limbatus*, and *G. bistriatus*, remained undescribed until recently (Loureço, 2003; Loureço *et al.*, 2004). Nevertheless, problems of faulty species identification remains possible in morphologically similar taxa, particularly those named in the early stages of the taxonomy of this genus. This is certainly the case for *G. madagascariensis* and *G. hirtus*.

*Grosphus madagascariensis* was described on the basis of one single specimen from Madagascar, without any indication of its precise collection locality. The type specimen, deposited in the Museum in Paris, has an associated original label with the distinct handwriting of Gervais reading "*S. goudotii*". A subsequent label written by Kraepelin is more precise and reads *S. goudotii* (*Androctonus*), Madagascar, Goudot. The name *goudotii* was not used in the original publication (Gervais, 1843) and the original label only seems to indicate an intention of Gervais to dedicate this species to the collector Jules Goudot. In Museum collections registration the following remark was written by Vachon: *Androctonus goudotii* Gervais, type = *Grosphus madagascariensis* (Gervais) 1844. The type specimen, presumably a male, is so poorly preserved that only metasomal characters can be observed. The illustrations given by Gervais (1843, 1844) are, however, clear enough to confirm the identity of this specimen as the type of *G. madagascariensis*. *G. hirtus* was described from a precise locality, Makaraingo in the central region of Madagascar, however, the type specimen is a juvenile female.

It is known that Jules Goudot travelled in the regions between the east coast, the region of Tamatave and Sainte-Marie Island. At the time of his journeys, other parts of Madagascar were inaccessible (forbidden) zones to foreign people (see Dorr, 1997 for details of Goudot's journeys). The region of Tamatave (Toamasina) was, and still is, one of the major harbours in Madagascar, a natural point of entry to the island. The Province of Toamasina was visited by Jules Goudot on several occasions while he stayed on Madagascar, so the specimen on which the description of *G. madagascariensis* was based was most probably collected somewhere in the eastern coastal region of the island.

Although *G. madagascariensis* and *G. hirtus* have overlapping areas of distribution, they inhabit different habitats. The first species is common in humid forests, whereas the second lives in more dry deciduous forests (Fage, 1929). Herein we redescribe both *G. madagascariensis* and *G. hirtus* based newly collected material from their typical habitats. One new species, closely associated to the *G. madagascariensis*/*G. hirtus* group, is described from a distinct forest habitat in northeastern Madagascar, the Forêt de Bobankora, E of Daraina in the Province d'Antsiranana.

## TAXONOMIC TREATMENT

BUTHIDAE C.L. Koch, 1837

*Grosphus* Simon, 1880*Grosphus madagascariensis* (Gervais, 1843)

Figs 1-4, 9-12

*Scorpio* (*Androctonus*) *madagascariensis* Gervais, 1843: 129.*Scorpio* (*Androctonus*) *madagascariensis* Gervais, 1844: 213.*Grosphus madagascariensis* Simon, 1880: 377.*Grosphus madagascariensis* Kraepelin, 1899: 33.*Grosphus madagascariensis* Kraepelin, 1900: 12.*Grosphus madagascariensis* Fage, 1929: 642.*Grosphus madagascariensis* Lourenço, 1996: 9.

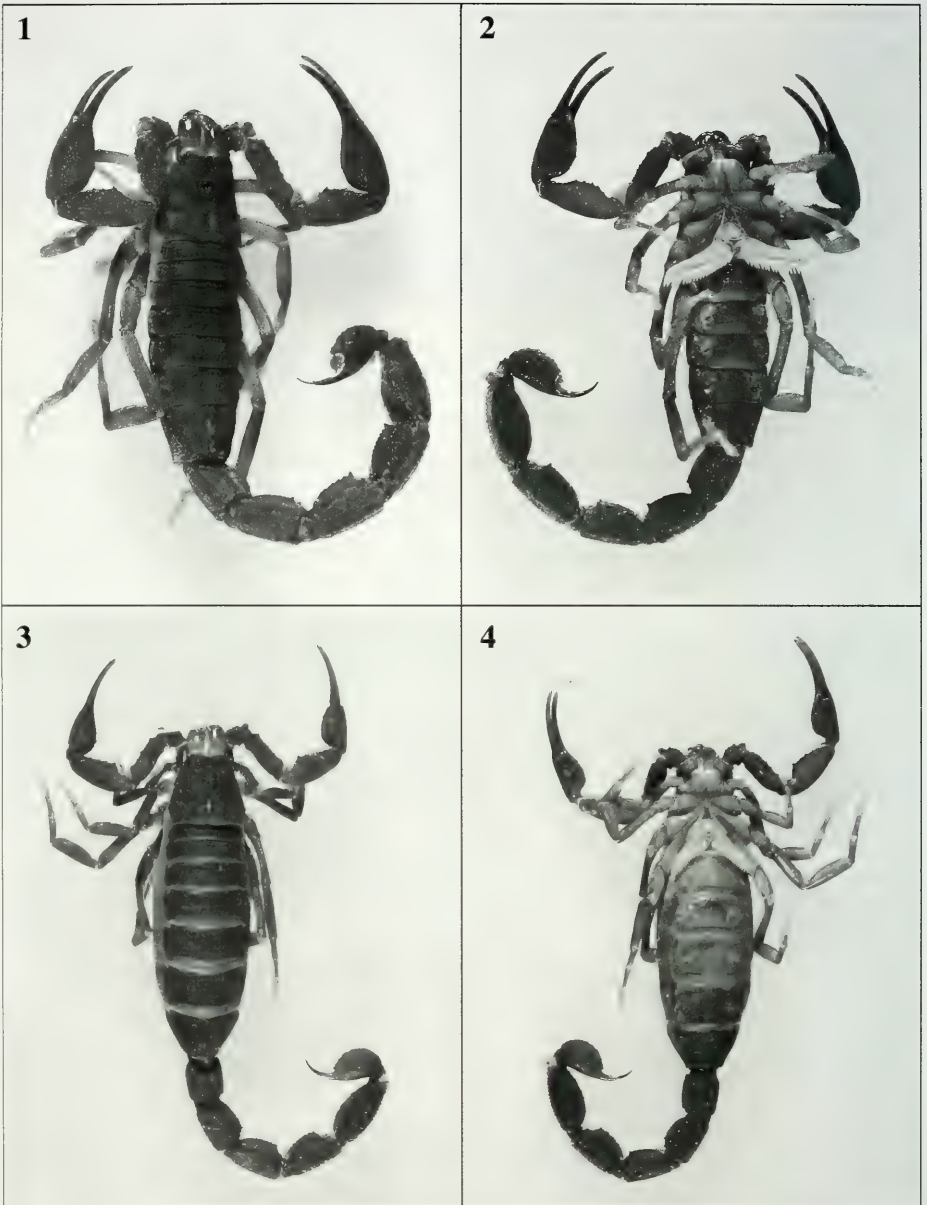
MATERIAL: Madagascar, Province de Toamasina, Forêt de Plateau de Makira, Forêt de Vohitaly, site F, 5 km SE village Anjahely, 15°26'58" S, 49°32'06" E, 540-680 m, 28/XII/2002, pitfall vial marked 'pitfall Vohitaly' (V. Andrianjakarivelo), 1 male, 1 female (MHNG).

REDESCRIPTION: (based on male and female, measurements in Table I)

Scorpion of medium size, with a total length of 45-60 mm. General coloration reddish brown to dark brown. Carapace and tergites brownish, in females darker than in males; eyes surrounded by black pigment. Metasoma: all segments reddish brown,

TABLE I. Comparative morphometric values (in mm) of the male and female of *Grosphus madagascariensis* and *G. hirtus* examined and of the male holotype of *G. goudoti* sp. n. and *G. simoni*.

	<i>G. madagascariensis</i>		<i>G. hirtus</i>		<i>G. goudoti</i> sp. n.	<i>G. simoni</i>
	M	F	M	F	M	M
Total length	45.4	52.5	38.9	48.8	59.8	54.2
Carapace:						
- length	5.5	6.2	4.8	6.1	7.2	6.4
- anterior width	4.0	4.4	3.4	4.3	5.3	4.8
- posterior width	6.6	7.6	5.8	6.9	7.9	6.9
Metasomal segment I:						
- length	3.5	4.1	2.8	3.3	5.2	4.5
- width	3.1	3.7	3.1	3.9	4.1	3.4
Metasomal segment V:						
- length	6.5	6.8	5.2	6.6	8.4	7.7
- width	3.1	3.2	2.7	4.1	3.4	3.2
- depth	3.0	3.3	2.8	3.5	3.4	3.3
Vesicle:						
- width	2.7	3.0	2.4	3.3	3.3	2.8
- depth	2.6	2.9	2.2	3.1	3.3	2.9
Pedipalp:						
- femur length	5.4	5.6	4.2	5.2	7.3	6.2
- femur width	1.7	1.9	1.4	1.8	2.2	1.9
- patella length	6.2	6.8	4.9	6.1	8.4	7.1
- patella width	2.5	2.6	2.1	2.7	2.9	2.7
- chela length	10.3	10.8	8.3	9.7	14.3	11.9
- chela width	2.8	2.5	2.5	2.5	3.9	3.1
- chela depth	2.5	2.4	2.3	2.4	3.5	2.8
Movable finger:						
- length	5.9	6.6	4.6	6.0	8.2	6.8



FIGS 1-4

*Grosphus madagascariensis*. 1-2. Male from Toamasina, dorsal and ventral aspects. 3-4. Female, idem.

with segments IV and V slightly darker; carinae blackish brown. Telson reddish brown; aculeus with reddish base and reddish brown tip. Venter: coxapophysis, sternum, genital operculum and pectines yellowish; sternites greenish yellow. Chelicerae



yellowish, with dark variegated pigmentation; fingers yellowish, with the teeth reddish. Pedipalps reddish, with vestigial variegated spots; legs yellowish in males and reddish in females, with diffused fuscous spots.

**Morphology.** Carapace moderately granular, more intensely so in females; anterior margin almost straight, with a very discrete median concavity. All carinae moderate to weak; furrows moderately to weakly developed. Median ocular tubercle anterior to centre of carapace; median eyes separated by a little more than one ocular diameter. Three pairs of lateral eyes. Sternum between sub-triangular and sub-pentagonal in shape. Mesosoma: tergites with minute moderately intense granulation. Median carina moderately to weakly developed on all tergites. Tergite VII pentacarinata. Venter: genital operculum consisting of two semi-oval plates. Pectines: pectinal teeth count 20-20 in male and 16-15 in female; basal middle lamella not dilated in males, strongly dilated in females. Sternites smooth, with weakly elongated stigmata. Metasoma: all segments longer than wide, with carinae strongly marked; segments I to III with 10 carinae, crenulate; segment IV with 8 carinae, crenulate. Segment V with 5 carinae. Dorsal carinae on segments II to IV with at least one posterior spinoid granule strongly developed. Intercarinal spaces weakly granular in males, more intensely granular in females. Telson with granules on latero-ventral and ventral surfaces; its dorsal surface smooth; aculeus weakly curved and shorter than the vesicle; subaculear tooth weak to vestigial. Cheliceral dentition characteristic of the family Buthidae (Vachon, 1963); two distinct small basal teeth present on the movable finger; ventral aspect of both fingers and of manus densely set with long setae. Pedipalps: femur pentacarinata; patella with dorsointernal and ventrointernal carinae and with several spinoid granules on the internal face; chela smooth, with vestigial carinae. Fixed and movable fingers with 11/13 oblique rows of granules. Trichobothriotaxy; orthobothriotaxy A- $\alpha$  (Vachon, 1974, 1975). Legs: tarsus with numerous short thin setae ventrally. Tibial spurs present on legs III and IV; pedal spurs present on legs I to IV; all spurs strong.

**ECOLOGY:** The specimens of *Grosphus madagascariensis* examined were collected in a distinct humid lowland forest of eastern Madagascar. The portion of the humid forest is close to the Masoala Peninsula, which receives on average almost 6 m of rainfall per year (Kremen, 2003).

In the Makira Forest, the site where the material was collected, the following species of scorpions were collected by V. Andrianjakarivelo with pit-fall devices during an inventory of small mammals of this region: *Grosphus madagascariensis*, *Grosphus simoni* Lourenço *et al.*, 2004 and *Tityobuthus baroni* (Pocock, 1890).

### ***Grosphus hirtus* Kraepelin, 1900**

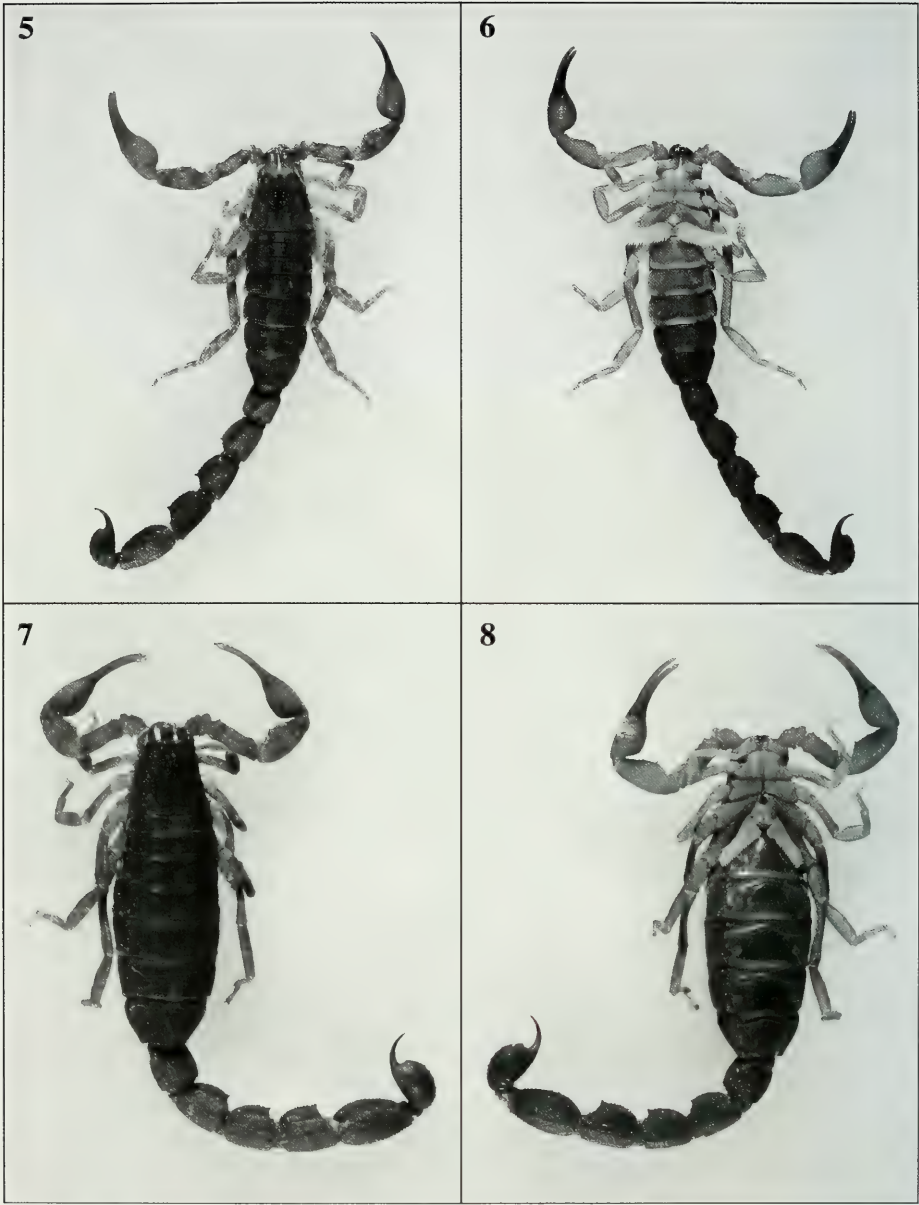
Figs 5-8, 13-15

*Grosphus hirtus* Kraepelin, 1900: 15.

*Grosphus hirtus* Fage, 1929: 645.

*Grosphus hirtus* Lourenço, 1996: 11.

**MATERIAL:** The adult specimens were collected in: Province of Mahajanga, Ankarafantsika Reserve, Forest station of Ampijoroa, Jardin Botanique A (pitfall traps), 16°18'S, 46°48'E, 24-27/II/2001 (G. Garcia Herrero), 1 male, 2 females, 36 juveniles. Juveniles were obtained in the laboratory during the study of the life cycle of the species (all in MHNG).

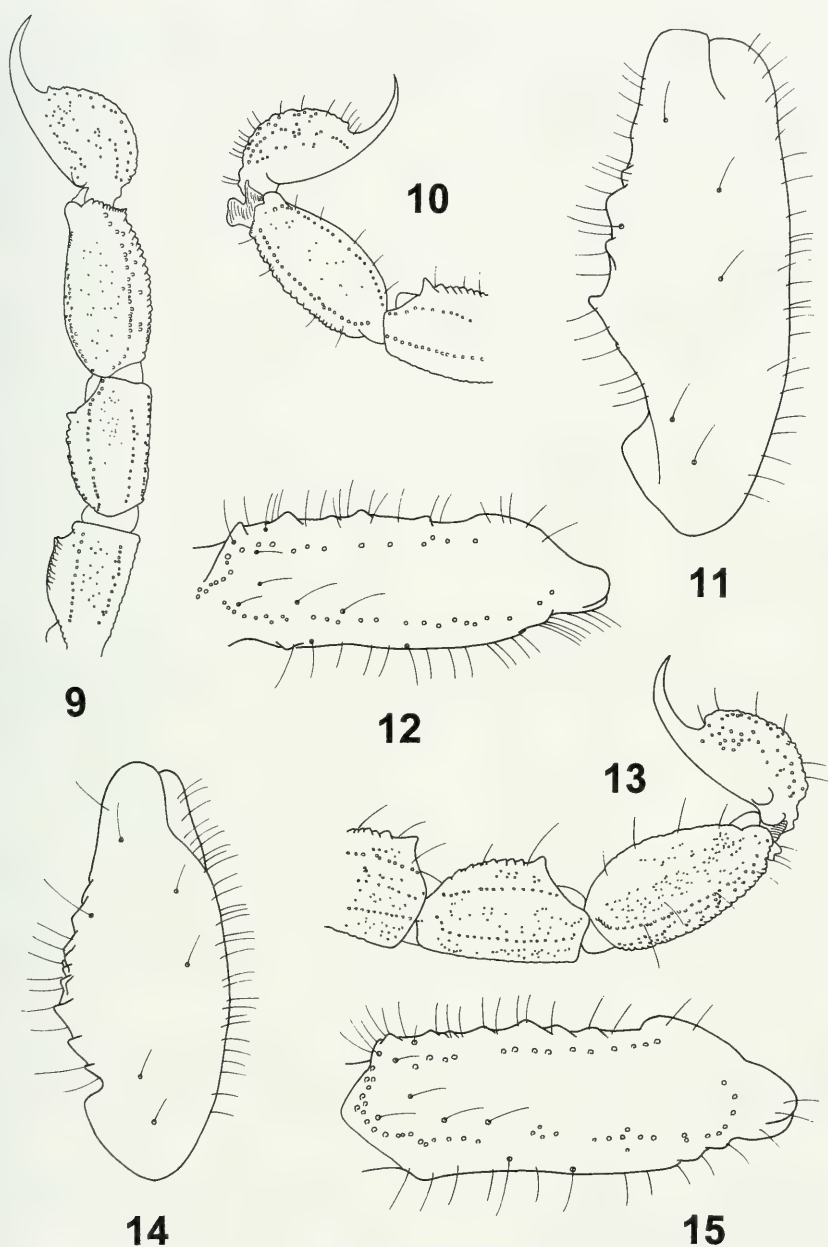


FIGS 5-8

*Grosphus hirtus*. 5-6. Male from Ankarafantsika, dorsal and ventral aspects. 7-8. Female, idem.

REDESCRIPTION: (based on male and females, measurements in Table I)

Scorpion of medium size with a total length of 40-50 mm. General coloration yellowish to reddish yellow, with variegated brownish spots over body and appendages. Carapace yellowish, with spots more marked on anterior and lateral edges;



FIGS 9-15

9-12. *Grosphus madagascariensis*. 9. Metasomal segments III-V and telson of male holotype, lateral aspect. 10. Metasomal segments IV-V and telson of male from Toamasina, lateral aspect. 11-12. Palpal patella and femur of male from Toamasina, dorsal aspect. 13-15. *Grosphus hirtus*, male from Ankarafantsika. 13. Metasomal segments III-V and telson, lateral aspect. 14-15. Palpal patella and femur, dorsal aspect.



eyes surrounded by black pigment. Mesosoma: yellowish, with confluent dark zones on the posterior edge of tergites. Metasoma: segments I to III yellowish; IV reddish yellow; V reddish; all segments with variegated dark pigmentation; dorsal aspect of segments I to IV each with a triangular spot. Telson reddish, without spots on carinae; aculeus with reddish base and dark reddish tip. Venter: coxapophysis, sternum, genital operculum and pectines yellowish; sternites dark yellow, with V to VII intensely spotted. Chelicerae yellowish, with dark variegated pigmentation throughout; fingers dark brown, with reddish teeth. Pedipalps: reddish yellow with variegated brownish spots. Legs yellowish, with diffused brownish spots.

**Morphology.** Carapace weakly granular in males, moderately granular in females; anterior margin almost straight, with a weak median concavity. All carinae and furrows weakly developed. Median ocular tubercle anterior to centre of carapace; median eyes separated by one ocular diameter. Three pairs of lateral eyes. Sternum sub-triangular in shape. Mesosoma: tergites with thin but intense granulation. Median carina moderately developed on all tergites. Tergite VII pentacarinat. Venter: genital operculum consisting of two subtriangular plates. Pectines: pectinal tooth count mostly 19-19 in males and 15-15 in females; basal middle lamellae not dilated in males, strongly dilated in females. Sternites smooth, with weakly elongated stigmata; VII with two vestigial carinae. Metasoma: segment I wider than long; segments I to III with 10 carinae, crenulate. Segment IV with 8 carinae, crenulate. Segment V with 5 carinae, crenulate. Dorsal carinae on segments II to IV each with one strong posterior spinoid granule. Intercarinal spaces strongly granular. Telson with a strong granulation on latero-ventral and ventral surfaces; its dorsal surface smooth; aculeus weakly curved and shorter than the vesicle; subaculear tooth vestigial. Cheliceral dentition characteristic of the family Buthidae (Vachon, 1963); two distinct basal teeth present on the movable finger; ventral aspect of both fingers and of manus densely set with long setae. Pedipalps: femur pentacarinat; patella with a dorsointernal carina and with several spinoid granules on the internal aspect; chela smooth, without carinae. Fixed and movable fingers with 11/12 oblique rows of granules. Trichobothriotaxy; orthobothriotaxy A- $\alpha$  (Vachon, 1974, 1975). Legs: tarsus with numerous short thin setae ventrally. Tibial spurs present on legs III and IV; pedal spurs present on legs I to IV; all spurs moderately to strongly developed.

**ECOLOGY:** The most common native forest formation of the Ankarafantsika region is a dry deciduous forest that occurs on a sandy substrate (Ramangason, 1988). The principal geological formation in the vicinity of the Ampijoroa Forest Station, which includes the Jardin Botanique A, is a plateau that rises to an elevation of 310-340 m above sea level, and this is most likely the zone where the *Grosphus hirtus* specimens treated in this paper were collected. Several different plants occurring in this habitat have varied adaptations to resist desiccation during the pronounced dry season, and different vertebrate species undergo hibernation or torpor to survive this period.

Annual precipitation in the Ankarafantsika area ranges from 1000-1500 mm, most of which falls between the months of November to April (Nicoll & Langrand, 1989). The month of January experiences the heaviest rainfall, with slightly less than 50% of the annual total. A very pronounced dry and cool period occurs between the months of May and September. During this latter period little to no rain falls and the

forest experiences a distinct drought. Monthly mean temperatures range from 17° to 35° C, and the annual average temperature is 26°C.

The scorpion fauna of the Forest Station of Ampijoroa, part of the Parc National d'Ankarafantsika, is composed of *Grosphus hirtus*, *G. ankarafantsika* Lourenço, 2003, *G. garciai* Lourenço, 2001, *Tityobuthus dastychi* Lourenço, 1997, and *Opisthacanthus madagascariensis* Kraepelin, 1894.

***Grosphus goudoti* sp. n.**

Figs 16-24

**MATERIAL:** Madagascar, Province d'Antsiranana, Forêt de Bobankora, versant ouest, site N° 2, 11 km E of Daraina (13°13.414'S, 49°45.586'E), 350-550 m (M. Raheriarisena & H. A. Rakotondravony), X/2002-III/2003, male holotype, deposited in the Muséum d'histoire naturelle, Genève.

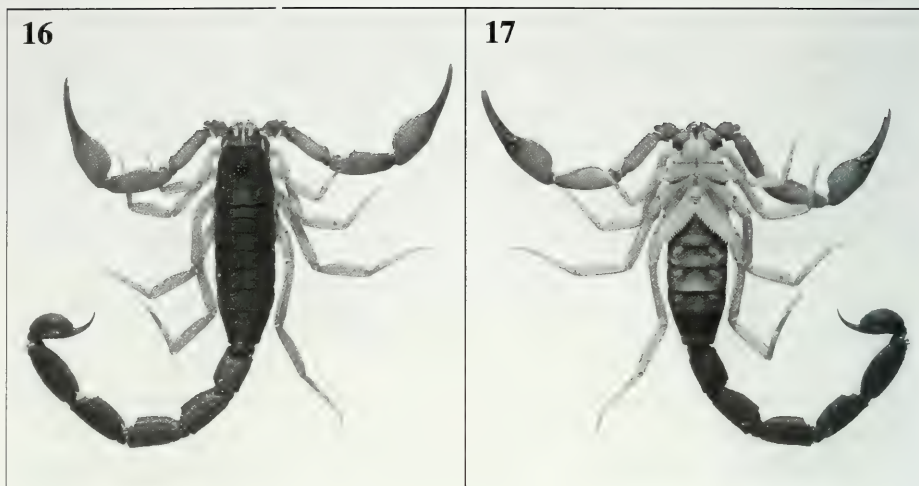
**ETYMOLOGY:** This patronym is in honor of Jules Goudot, collector of the first *Grosphus* species in Madagascar.

**DIAGNOSIS:** Scorpions of medium size, with a total length of 60 mm. General coloration reddish brown to dark brown. Certain morphological characters indicate that *G. goudoti* sp. n. is close to the *G. madagascariensis*/*G. hirtus* group, and in particular to *G. simoni* Lourenço, Goodman & Ramilijaona, 2004 but it can be readily distinguished from the last species by the following characters: (i) a much darker coloration of carapace and tergites, with the presence of one inverted black triangle in the anterior zone of the carapace, stretching from the lateral eyes to the median eyes; (ii) the teeth of pectines longer than in *G. simoni*; (iii) dorsal carinae of metasomal segments II to IV without any posterior spinoid granules.

**DESCRIPTION:** (based on male holotype, measurements in Table I)

**Coloration.** Basically reddish brown to dark brown. Prosoma: carapace reddish brown with one inverted black triangle in the anterior zone of the carapace, stretching from the lateral eyes to the median eyes; eyes surrounded by black pigment. Mesosoma: reddish brown, with dark strips on posterior margins of tergites. Metasoma: segments I to III reddish brown; IV-V dark brown; all segments with some vestigial dark pigmentation on carinae. Telson reddish brown, with dark zones on granulations; aculeus with reddish brown base and dark brown tip. Venter: coxapophysis, sternum, genital operculum and pectines yellowish; sternites yellow with greenish zones; VII dark brown. Chelicerae reddish yellow, with dark variegated pigmentation on the entire surface; fingers reddish brown; teeth reddish. Pedipalps: reddish to reddish brown; chela fingers dark brown. Legs yellowish, with very diffused variegated spots.

**Morphology.** Carapace covered with a thin but intense granulation; anterior margin almost straight, with a very weak median concavity. All carinae weak; furrows moderately developed. Median ocular tubercle anterior to centre of carapace; median eyes separated by one ocular diameter. Three pairs of lateral eyes. Sternum sub-triangular in shape. Mesosoma: tergites with thin but intense granulation. Median carina moderately developed on all tergites. Tergite VII pentacarinat. Venter: genital operculum consisting of two semi-oval plates. Pectines: pectinal tooth count 19-19, basal middle lamellae of each pecten not dilated in males. Sternites smooth, with moderate-



FIGS 16-17

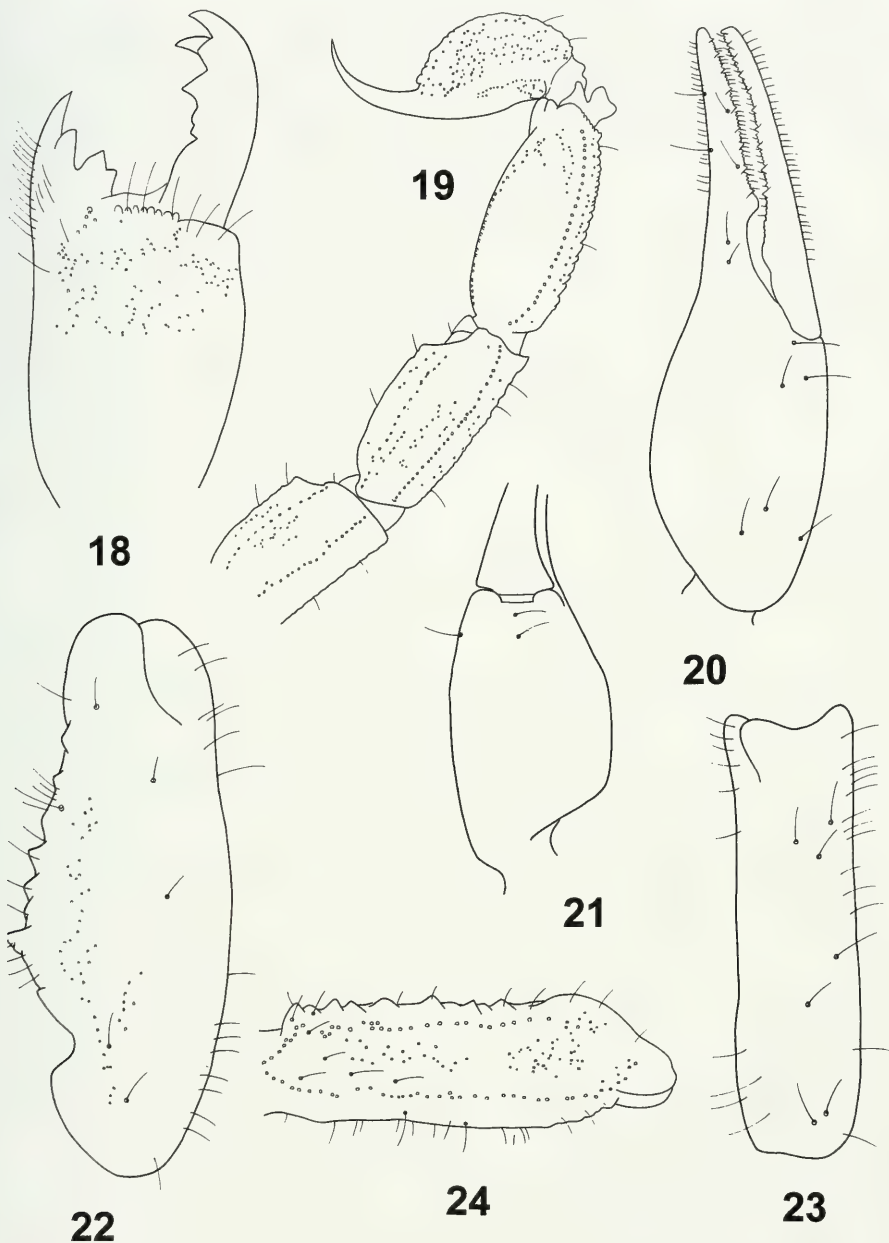
*Grosphus goudoti* sp. n. Male holotype, dorsal and ventral aspects.

ly elongated spiracles; VII with four weak carinae. Metasoma: segments I and II with 10 carinae, moderately crenulate; segments III and IV with 8 carinae, weakly crenulate. Segment V with 5 carinae. Dorsal carinae on segments II to IV without any posterior spinoid granules. Intercarinal spaces moderately to weakly granular. Telson moderately granular over latero-ventral and ventral surfaces; its dorsal surface smooth; aculeus moderately curved and shorter than the vesicle; subaculear tooth vestigial. Cheliceral dentition characteristic of the family Buthidae (Vachon, 1963); two distinct basal teeth present on the movable finger; ventral aspect of both fingers and of manus densely set with long setae. Pedipalps: femur pentacarinat; patella with dorsointernal and ventralinternal carinae and with some strong spinoid granules on the internal aspect; chela smooth, without carinae. Fixed and movable fingers with 11/12 oblique rows of granules. Trichobothriotaxy; orthobothriotaxy A- $\alpha$  (Vachon, 1974, 1975). Legs: tarsus with numerous short thin setae ventrally. Tibial spurs present on legs III and IV; pedal spurs present on legs I to IV; all spurs strong.

Female unknown.

**ECOLOGY:** The site where the holotype of *Grosphus goudoti* sp. n. was collected is in a forested area forming an exceptional zone of ecotonal transition in the central portion of northern Madagascar. This is known as the Daraina Forest, named after the largest local village. This area is biotically very complex and the remaining forests are greatly reduced in size and fragmented. In a distance of a few kilometres there are transitions between dry deciduous forest formations prevailing in the west and humid forests prevailing in the east. Elevation, aspect, soil type, and distance to the sea are important parameters associated with these transitions. The site where the holotype of *G. goudoti* sp. n. was collected is composed of dry deciduous lowland forest





FIGS 18-24

*Grosphus goudoti* sp. n. Male holotype. 18. Chelicera, dorsal aspect. 19. Metasomal segments III-V and telson, lateral aspect. 20-24. Trichobothrial pattern of pedipalp. 20-21. Chela, dorso-external and ventral aspects. 22-23. Patella, dorsal and external aspects. 24. Femur, dorsal aspect.



FIG. 25

Map of Madagascar, with indication of the sites where *Grosphus madagascariensis* and *G. hirtus* have been collected, and the locality of the new *Grosphus* species. *G. madagascariensis* (black star), *G. hirtus* (black circle), and *G. goudoti* sp. n. (black circle with white star).

that is relatively intact, with little leaf litter, relatively open understory, which rests on reddish lateritic soils.

Other species of scorpions known to occur in the forests of the Daraina area are *Heteroscorpion magnus* Lourenço & Goodman, 2002, *Tityobuthus darainensis* Lourenço & Goodman, 2002, and *Grosphus darainensis* Lourenço, Goodman & Ramilijaona, 2004 (Lourenço and Goodman, 2002; Lourenço *et al.*, 2004).

#### KEY TO THE SPECIES OF THE GENUS *GROSPHUS*

- |   |   |   |
|---|---|---|
| 1 | Pectines with a maximum of 21 teeth . . . . .   | 2 |
| - | Pectines with more than 22 teeth . . . . .  | 7 |
| 2 | Coloration yellowish to reddish brown; variegated brownish pigmentation present . . . . .                   | 3 |
| - | Coloration from yellowish to reddish brown or dark brown; variegated brownish pigmentation absent . . . . . | 4 |

- 3 Coloration reddish brown; adult body length 30 mm . . . . . *G. garciai*  
 - Coloration yellowish; adult body length 40-50 mm . . . . . *G. hirtus*
- 4 Metasomal segments II-IV with one or more spinoid posterior granules . . . . . 5  
 - Metasomal segments II-IV without any spinoid granule . . . . . *G. goudoti* sp. n.
- 5 Metasomal segments II-IV with one spinoid posterior granule . . . . . 6  
 - Coloration reddish yellow; dorsal carinae of metasomal segments II-IV  
 with 2 to 6 strong spinoid posterior granules . . . . . *Grosphus simoni*
- 6 Coloration yellowish; dorsal carinae of metasomal segments II-IV with  
 one small spinoid posterior granule . . . . . *Grosphus darainensis*  
 - Coloration reddish to dark brown; metasomal segments II-IV with one  
 strong spinoid posterior granule . . . . . *G. madagascariensis*
- 7 Coloration blackish or reddish brown to yellowish; pectines with 30 to  
 40 teeth; adult body length more than 90 mm . . . . . 8  
 - Coloration reddish brown to yellowish, never blackish; adult body  
 length less than 90 mm . . . . . 9
- 8 Coloration blackish throughout . . . . . *G. grandidieri*  
 - Coloration reddish brown to yellowish . . . . . *G. ankarana*
- 9 Mesosoma with homogenous coloration, reddish brown or yellowish . . . . . 10  
 - Mesosoma with a blackish longitudinal median band, or with two  
 blackish longitudinal lateral bands . . . . . 15
- 10 Adult total length more than 65 mm; mesosoma reddish brown . *G. flavopiceus*  
 - Adult total length less than 60 mm; mesosoma dark yellow; metasomal  
 segment V and telson with or without blackish spots . . . . . 11
- 11 Metasomal segments and telson without blackish spots . . . . . 12  
 - Metasomal segments and telson totally blackish or with blackish spots . . . . . 13
- 12 Metasomal segments yellowish, with moderately to strongly developed  
 carinae on II to IV . . . . . *G. intertidalis*  
 - Metasomal segments reddish yellow; rounded and with vestigial carinae  
 . . . . . *Grosphus mahafaliensis*
- 13 Metasomal segment V and telson with blackish spots . . . . . *G. annulatus*  
 - Metasomal segment V and telson totally blackish . . . . . 14
- 14 Telson with aculeus of the same length or shorter than the vesicle . . . . . *G. feti*  
 - Telson with aculeus longer than the vesicle . . . . . *G. olgae*
- 15 Mesosoma with a wide blackish longitudinal median band; basal middle  
 lamellae of female pectines three times longer than wide at their base  
 and covering the four proximal teeth . . . . . *G. limbatus*  
 - Mesosoma with two narrow blackish longitudinal lateral bands . . . . . 16
- 16 Carapace without a blackish triangular spot; basal middle lamellae of  
 female pectines weakly curved, widening in proximal half and covering  
 the two proximal teeth . . . . . *G. bistriatus*  
 - Carapace with a blackish triangular spot; basal middle lamellae of the  
 female pectines curved and constantly narrowing from the base to apex,  
 covering the four proximal teeth . . . . . *G. ankarafantsika*



## ACKNOWLEDGEMENTS

We are grateful to Mr Cl. Ratton and Mrs Florence Marteau, Natural History Museum, Geneva for the preparation of the photos, and the arrangements of the plates, respectively. A portion of the material used in this study was obtained during field missions financed by the Volkswagen Foundation and Conservation International.

## REFERENCES

- DORR, L. J. 1997. Plant collectors in Madagascar and the Comoro Islands. *Kew: Royal Botanic Gardens*, XLVI + 524 pp.
- FAGE, L. 1929. Les Scorpions de Madagascar. Faune des Colonies françaises 3. *Société d'Editions Géographiques Maritimes Coloniales*, Paris, pp. 637-694.
- GERVAIS, P. 1843. Les principaux résultats d'un travail sur la famille des Scorpions. *Société philomatique de Paris. Extraits des procès-verbaux des séances* 5 (7): 129-131.
- GERVAIS, P. 1844. Remarques sur la famille des Scorpions. *Archives du Muséum d'Histoire Naturelle*, Paris 4: 201-240.
- KRAEPELIN, K. 1899. Scorpiones und Pedipalpi. In: F. DAHL (ed). Das Tierreich. Herausgegeben von der Deutschen zoologischen Gesellschaft. 8 (Arachnoidea). R. Friedländer und Sohn Verlag, Berlin, 265 pp.
- KRAEPELIN, K. 1900. Ueber einige neue Gliederspinnen. *Abhandlungen aus dem Gebiete der Naturwissenschaften. Herausgegeben vom naturwissenschaftlichen Verein in Hamburg* 16, 1 (4): 1-17.
- KREMEN, C. 2003. The Masoala Peninsula (pp. 1459-1466). In: GOODMAN, S. M. & BENSTEAD, J. P. (eds). The natural history of Madagascar. *The University of Chicago Press*, Chicago.
- LOURENÇO, W. R. 1996. Scorpions. Faune de Madagascar. *Muséum national d'Histoire naturelle*, Paris, 102 pp.
- LOURENÇO, W. R. 2003. New taxonomic considerations on some species of the genus *Grosphus* Simon, with description of a new species (Scorpiones, Buthidae). *Revue suisse de Zoologie* 110 (1): 141-154.
- LOURENÇO, W. R. & GOODMAN, S. M. 2002. Scorpions from the Daraina region of northeastern Madagascar with special reference to the family Heteroscorpionidae Kraepelin, 1905. *Revista Ibérica de Aracnologia* 6: 53-68.
- LOURENÇO, W. R. & GOODMAN, S. M. 2003. Description of a new species of *Grosphus* Simon (Scorpiones, Buthidae) from the Ankarana Massif, Madagascar. *Revista Ibérica de Aracnologia* 7: 19-28.
- LOURENÇO, W. R., GOODMAN, S. M. & RAMILJAONA, O. 2004. Three new species of *Grosphus* Simon from Madagascar (Scorpiones, Buthidae). *Revista Ibérica de Aracnologia* 9: 225-234.
- NICOLL, M. E. & LANGRAND, O. 1989. Madagascar. *Revue de la conservation et des aires protégées*. WWF, Gland, Switzerland, XVII + 374 pp.
- RAMANGASON, G. S. 1988. Flore et végétation de la Forêt d'Ampijoroa (pp. 130-137). In: RAKOTOVAO, L., BARRE, V. & SAYER, J. (eds). L'équilibre des écosystèmes forestiers à Madagascar. *IUCN, Gland*.
- SIMON, E. 1880. Etudes arachnologiques, 12<sup>e</sup> Mémoire (1). XVIII. Descriptions de genres et espèces de l'ordre des Scorpiones. *Annales de la Société entomologique de France*, sér. 5, 10: 377-398.
- VACHON, M. 1963. De l'utilité, en systématique, d'une nomenclature des dents des chélicères chez les Scorpions. *Bulletin du Muséum national d'Histoire naturelle*, Paris, 2<sup>e</sup> sér., 35 (2): 161-166.

- VACHON, M. 1974. Etude des caractères utilisés pour classer les familles et les genres de Scorpions (Arachnides). 1. La trichobothriotaxie en arachnologie. Sigles trichobothriaux et types de trichobothriotaxie chez les Scorpions. *Bulletin du Muséum national d'Histoire naturelle, Paris*, 3e sér., n° 140, Zool. 104: 857-958.
- VACHON, M. 1975. Sur l'utilisation de la trichobothriotaxie du bras des pédipalpes des Scorpions (Arachnides) dans le classement des genres de la famille des Buthidae Simon. *Comptes Rendus des Séances de l'Académie des Sciences* 281 (D): 1597-1599.





***Vitronura mascula*, a new species of Neanurinae  
(Collembola: Neanuridae) from northern Vietnam, with a key  
to the species of the genus**

Adrian SMOLIS<sup>1</sup> & Louis DEHARVENG<sup>2</sup>

<sup>1</sup>Zoological Institute, University of Wrocław, Przybyszewskiego 63/77,  
51-148 Wrocław, Poland. E-mail: adek@biol.uni.wroc.pl

<sup>2</sup>Museum National d'Histoire Naturelle, Laboratoire d'Entomologie, FRE2695 du  
CNRS, 45 rue Buffon, F-75005 Paris, France. E-mail: deharven@mnhn.fr

***Vitronura mascula*, a new species of Neanurinae (Collembola:  
Neanuridae) from northern Vietnam, with a key to the species of the  
genus.** - A new species of the genus *Vitronura* Yosii, 1954 sensu Cassagnau,  
1986 from northern Vietnam is described and illustrated. An identification  
key for all the known species of the genus is given.

**Keywords:** Collembola - Neanuridae - taxonomy - Vietnam.

## INTRODUCTION

Yosii (1969) established the subgenus *Vitronura* in the genus *Neanura* MacGillivray, 1893 and designated *Neanura mandarina* Yosii, 1954 from Japan as its type species. Cassagnau (1980) raised *Vitronura* to generic status and later (1983) classified the taxon to a lineage of blasconurian Neanurinae. At present the genus is included in the tribe Paleonurini (Cassagnau, 1989). The presence of separate tubercles Fr and An on dorsal side of the head distinguish *Vitronura* from all genera of Paleonurini. As presently defined, the genus comprises 14 species, occurring mainly in Southeast and Eastern Asia.

Till now only one cosmopolitan species, *V. giselae* (Gisin, 1950), was recorded from Vietnam (Nguyen, 1995). Examination of the material of Collembola from northern Vietnam revealed one new species of the genus. The present paper contains its description and an updated key to all members of the genus.

## TERMINOLOGY

The terminology and layout of the tables used in this paper follow Deharveng (1983), Deharveng & Weiner (1984) and Greenslade & Deharveng (1990), and the following abbreviations are used:

GENERAL MORPHOLOGY: abd. – abdomen, ant. – antenna, Cx – coxa, Fe – femur, Scx2 - subcoxa 2, T – tibiotarsus, th. – thorax, Tr – trochanter, VT – ventral tube.

GROUPS OF CHAETAE: Ag – antegenital, An. – anal, Fu – furcal, Ve – ventroexternal, Vi – ventrointernal, VI – ventrolateral.

TUBERCLES: An – antennal, Fr – frontal, Cl – clypeal, De – dorsoexternal, Di – dorsointernal, DI – dorsolateral, L – lateral, Oc – ocular, So – subocular.

TYPES OF CHAETAE: Ml – long macrochaeta, Mc – short macrochaeta, me – mesochaeta, mi – microchaeta, ms – s-microchaeta, S – or s – chaeta sensuality or sensillum, or – organite of antenna IV, i – ordinary chaeta on antenna IV, mou – thin cylindrical sensilla on ant. IV („soies mousses”), x – labial papilla x.

## DESCRIPTION OF THE NEW SPECIES

### *Vitronura mascula* sp. n.

TYPE MATERIAL: Holotype, adult male on slide; northern Vietnam, Tam Dao National Park, the top of Tam Dao mount (1300 m. a. s. l.), 08.04.1997, mosses and lichens on rhododendron branches, leg. R. J. Pomorski. Paratype, 1 subadult male, the same data as holotype. Holotype is preserved in collection of the Department of Biodiversity and Evolutionary Taxonomy, Wrocław University, Poland; paratype housed in the collection of the Muséum d'histoire naturelle in Geneva.

ETYMOLOGY: Among known members of the genus, only males of the new species have male (Latin word "masculus") ventral organ.

DIAGNOSIS: *Vitronura mascula* sp. n. differs from other *Vitronura* species in the presence of male ventral organ and strong reduction of dorsal chaetotaxy on head (absence of chaetae: O, C, D, E, Oca, Ocp, Di2, De2). In addition the new species is characterised by ogival labrum, claw without inner denticle and separate tubercles Di on head and abd. V.

DESCRIPTION: Body length (without antennae): holotype - 1.05 mm, paratype - 1.1 mm. Habitus typical of *Paleonurini* (Cassagnau, 1989). Tertiary granulation well developed. Colour of the body in alcohol white. 2+2 unpigmented eyes (Fig. 1).

Types of dorsal ordinary chaetae: macrochaetae Ml thickened, moderately long, narrowly sheathed, the distal three-fourth densely furnished with short pointed scale-like (teeth) which are extremely dense at the tip (Fig. 4), macrochaetae Mc with similar morphology, microchaetae very short, smooth, without teeth.

Head. Buccal cone slightly elongate. Labrum pointed, with ventral sclerifications ogival as in Figs 2, 3. Labrum chaetotaxy 0 / 2, 4. Chaetotaxy of labium as in Fig. 3 and Tab. 1a. Maxilla styliform, mandible thin and tridentate. Chaetotaxy of antennae as in Tab. 1a. Apical bulb distinct, trilobed. S-chaetae subequal, long and moderately thickened. Chaetotaxy of head as in Fig. 1 and in Tab. 1a. Chaeta O absent.

Thorax, abdomen, legs. Chaetotaxy of th. and abd. as in Figs 1, 8 and in Tab. 1b. Tubercles Di on th. II-III with 2 chaetae. Male ventral organ fully developed only in adult male with ductus ejaculatorius (in subadult poorly visible), built of thickened and slightly forked chaetae on abdominal sterna III, IV, V and VI (Fig. 8). Chaetae of ventral organ in subadult with similar morphology as microchaetae (not thickened and not forked), but with distinctly greater chaetopor (Fig. 6). Tubercles L on abd. IV and

Table 1. Chaetotaxy of *Vitronura muscula* sp. n.

## a) Cephalic chaetotaxy

Tubercle	Number of chaetae	Types of chaetae	Names of chaetae
Cl	4	Ml mi	F G
An	1	Ml	B
Fr	2	Ml	A
Oc	1	Ml	Ocm
Di	1	Ml	Di1
De	1	Ml	De1
(Dl+L+So)	9	Ml, Mc, mi	impossible to recognise

Number of other cephalic chaetae: Vi, 5; Ve, 7; labrum, 0 / 2, 4; labium, 9, 0x; ant. I, 7; ant. II, 11; ant. III, 17 + 5s; ant. IV, 8S + i + or + 12mou.

## b) Postcephalic chaetotaxy

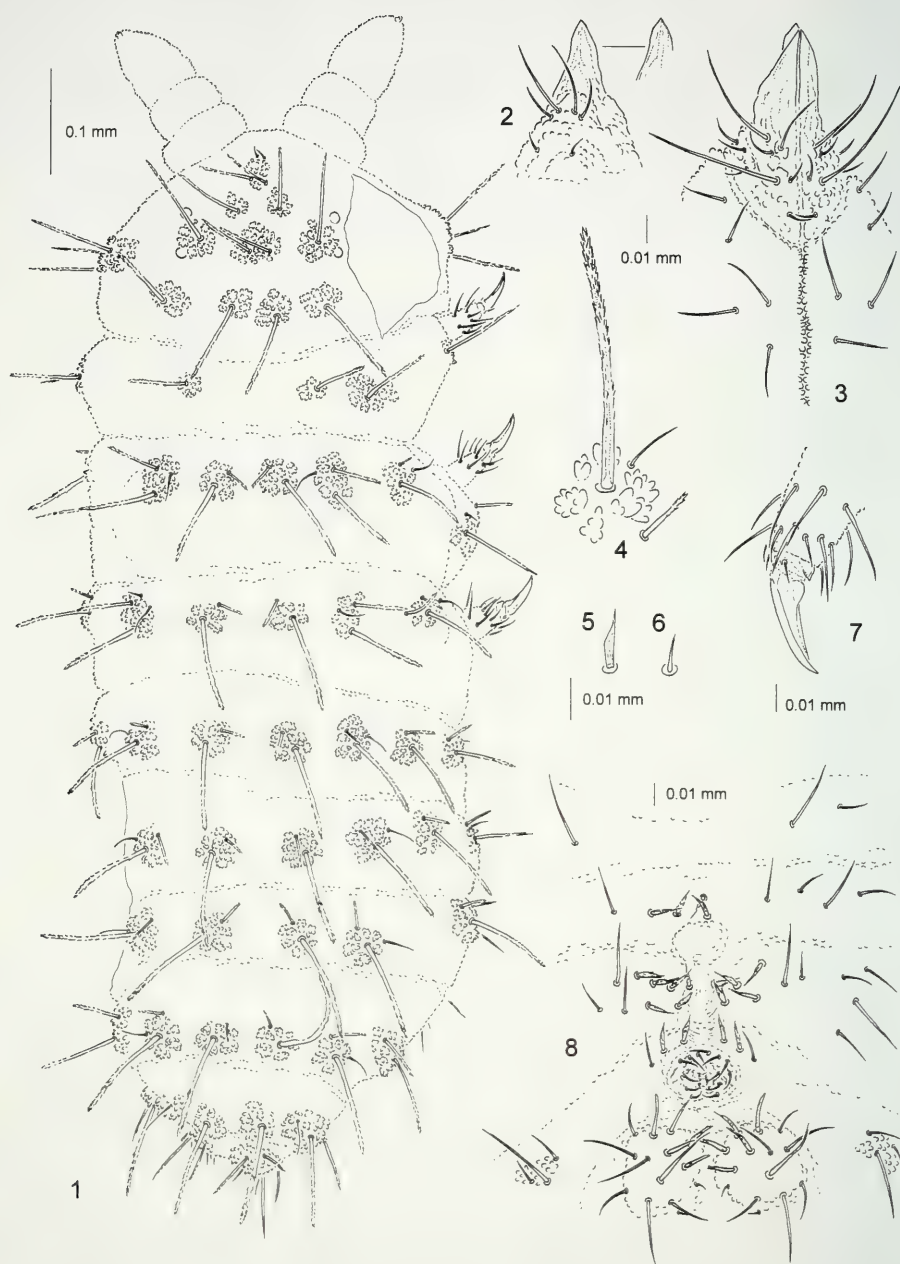
	Terga						Legs		
	Di	De	Dl	L	Scx2	Cx	Tr	Fe	T
th. I	1	1(2)	1	-	0	3	6	13	18
th. II	2	2+s	2+s+ms	3	2	7	6	12	18
th. III	2	3+s	3+s	3	2	8	6	11	17
Sterna									
abd. I	2	2+s	2	3	VT: 4	Ve1- absent			
abd. II	2	2+s	2	3	Ve: 2				
abd. III	2	2+s	2	3	Ve: 3-4				
abd. IV	2	2+s	2	5	Ve: 8-9			Fu:4 me	0 mi
abd. V	1(2)	5+s		3	Ag: 3			Vl: 4	
abd. VI		7			Ve:14		An.: 2mi		

V respectively with 5 and 3 chaetae (Fig. 5). Cryptopygy absent. Chaetotaxy of legs as in Tab. 1b. Claw relatively long, without inner tooth (Fig. 7).

REMARKS: The new species appears to be the closest to *V. tubercula* Lee & Kim, 1990 from Taiwan, because both species have similar morphology of macrochaetae and claws without teeth. *Vitronura muscula* sp. n. differs from the mentioned species in separate tubercles Di on head (in *tubercula* fused), number of chaetae Di of th. II-III (in *muscula*: 2, in *tubercula*: 3) and number of chaetae De of abd. I-III (in *muscula*: 2+s, in *tubercula*: 3+s).

The genus *Vitronura* was first keyed by Cassagnau & Deharveng (1981). Changes in definition of the genus (Cassagnau, 1986) and four species described after that date make it necessary to elaborate an updated key. The key includes among others species *Vitronura giselae*, *V. mandarina* and *V. dentata*, which were formally synonymized by Yoshii (1995). This author considered *V. giselae* and *V. mandarina* as synonyms of *rosea*, a species very succinctly described from Paris by Gervais in 1842; two species of yellow to pink color exist there, i.e. *Vitronura "giselae"* Gisin and





FIGS 1-8

*Vitronura mascula* sp. n.: 1 - habitus and dorsal chaetotaxy (holotype), 2 - chaetotaxy of labrum, 3 - chaetotaxy of labium and group VI, 4 - tubercle De of abd. IV, 5 - chaeta of male ventral organ (adult male), 6 - chaeta of male ventral organ (subadult male), 7 - tibiotarsus and claw of legs III (lateral view), 8 - chaetotaxy of abdominal sterna II-VI.

*Monobella grassei* Denis, and there is no conclusive evidence that *rosea* correspond to one rather than the other of them. We therefore continue to consider *Anoura rosea* Gervais, 1842 as species inquirenda. As differential characters between *giselae* and *mandarina* are not discussed by Yoshii, the synonymy he proposed cannot be accepted at the moment. For the same reason, the synonymy between *dentata* Deharveng & Weiner, 1983 and *pygmaea* Yosii, 1954 proposed in the same paper (Yoshii, 1995) cannot be retained. Differential characters between these species are given in the key.

#### KEY TO THE SPECIES OF THE GENUS *VITRONURA*

- 1   Tubercle Oc on head with 1 or 2 chaetae ..... 2
- Tubercle Oc on head with 3 chaetae ..... 10
- 2   Tubercle Oc on head with 1 chaeta ..... *V. mascula* sp. n.
- Tubercle Oc on head with 2 chaetae ..... 3
- 3   Tubercles Di on head fused along midline . . . . *V. tubercula* Lee & Kim, 1990
- Tubercles Di on head separate ..... 4
- 4   Chaeta O on head present ..... 7
- Chaeta O on head absent ..... 5
- 5   Tubercles Di on abd. V fused along midline ..... *V. sinica* Yosii, 1976
- Tubercles Di on abd. V separate ..... 6
- 6   Tubercle De of th. V with 5 chaetae ..... *V. luzonica* Yosii, 1976
- Tubercle De of th. V with 4 chaetae *V. gressitti* Cassagnau & Deharveng, 1981
- 7   Tubercle Di of th. I with 2 chaetae ..... *V. latior* (Rusek, 1967)
- Tubercle Di of th. I with 1 chaeta ..... 8
- 8   Claw with inner denticle ..... 9
- Claw without inner denticle ..... *V. mandarina* (Yosii, 1954)
- 9   Tubercle Di of abd. V with 2 chaetae ..... *V. namhaiensis* (Lee, 1974)
- Tubercle Di of abd. V with 3 chaetae ..... *V. pygmaea* (Yosii, 1954)
- 10   Tubercle De on head with 2 chaetae ..... *V. joanna* (Coates, 1968)
- Tubercle De on head with 3 chaetae ..... 11
- 11   Tubercles Di on head fused along midline ..... 12
- Tubercles Di on head separate ..... 13
- 12   Chaeta O on head present ..... *V. macgillvrayi* (Denis, 1933)
- Chaeta O on head absent ..... *V. singaporiensis* (Yossi, 1956)
- 13   Claw with inner denticle ..... *V. dentata* Deharveng & Weiner, 1984
- Claw without inner denticle ..... 14
- 14   Labrum distally ogival ..... *V. acuta* Deharveng & Weiner, 1984
- Labrum non-ogival ..... *V. giselae* (Gisin, 1950)

#### ACKNOWLEDGEMENTS

We are greatly indebted to Prof. Romuald J. Pomorski for the loan of material of *V. mascula*. Specimens of the species were collected during faunistic investigations of North Vietnam, sponsored by Museum and Institute of Zoology PAS (Warsaw) and Wrocław University (project number 1018/W/IZ/97). The studies of this material were financed by the University of Wrocław (project number 2020/W/IZ/2001).

## REFERENCES

- CASSAGNAU, P. 1980. Nouveaux critères pour un redécoupage phylogénétique des Collemboles Neanurinae (s. Massoud 1967). *In*: DALLAI, R. (ed.). 1st International Seminar on Apterygota, Siena 1978: 115-132.
- CASSAGNAU, P. 1983. Un nouveau modèle phylogénétique chez les Collemboles neanurinae. *Nouvelle Revue d'Entomologique* 13: 3-27.
- CASSAGNAU, P. 1986. Sur l'évolution des Neanurinae paucituberculés à pièces buccales réduites (Collemboles). *In*: DALLAI, R. (ed.). 2nd International Seminar on Apterygota, Siena: 313-317.
- CASSAGNAU, P. 1989. Les Collemboles Neanurinae; éléments pour une synthèse phylogénétique et biogéographique (pp.171-182). *In*: DALLAI, R. (ed.). 3rd International Seminar on Apterygota, Siena: 171-182.
- CASSAGNAU, P. & DEHARVENG, L. 1981. Sur le genre *Vitronura* (Collemboles Neanuridae): aspect systématique et approche cytogénétique. *Bulletin du Muséum National d'Histoire Naturelle, Paris* 4 (3): 151-173.
- DEHARVENG, L. 1983. Morphologie évolutive des Collemboles Neanurinae en particulier de la lignée Neanurinae. *Travaux du Laboratoire d'Écobiologie des Arthropodes Edaphiques, Toulouse* 4 (2): 1-63.
- DEHARVENG, L. & WEINER, W. 1984. Collemboles de Corée du Nord III - Morulinae et Neanurinae. *Travaux du Laboratoire d'Écobiologie des Arthropodes Edaphiques, Toulouse* 4 (4): 1-61.
- GREENSLADE, P. & DEHARVENG, L. 1990. Australian species of the genus *Australonura* (Collembola, Neanuridae). *Invertebrate Taxonomy* 3: 565-593.
- LEE, B-H. & KIM, J-T. 1990. Systematic Studies on Chinese Collembola (Insecta) II. Five New Species and Two New Records from Taiwan in the Family Neanuridae. *The Korean Journal of Systematic Zoology* 6 (2): 235-250.
- NGUYEN TRI TIEN, 1995. Species composition and structure of Collembola in North Vietnam. *In*: Selected collection of scientific reports on ecology and biological resources. *Vietnam National Center for Natural Science and Technology, Institute of Ecology and Biological Resources, Hanoi*: 578-585.
- YOSHII, R. 1995. Identity of some Japanese Collembola III. *Acta Zoologica Asiae Orientalis* 3: 50-68.
- YOSHII, R. 1969. Collembola-Arthropleona of the IBP-Station in the Shiga Heights, Central Japan, I. *Bulletin of the National Science Museum Tokyo* 12 (3): 531-556.



## The Palaearctic trioizids associated with Rubiaceae (Hemiptera, Psylloidea): a taxonomic re-evaluation of the *Trioza galii* Foerster complex

Daniel BURCKHARDT<sup>1</sup> & Pavel LAUTERER<sup>2</sup>

<sup>1</sup> Naturhistorisches Museum, Augustinergasse 2, CH-4001 Basel, Switzerland.

E-mail: daniel.burckhardt@unibas.ch

<sup>2</sup> Moravian Museum, Department of Entomology, Hviezdoslavova 29a,

CZ-62700 Brno-Slatina, Czech Republic. E-mail: ento.laut@volny.cz

### The Palaearctic trioizids associated with Rubiaceae (Hemiptera, Psylloidea): a taxonomic re-evaluation of the *Trioza galii* Foerster complex.

- The Palaearctic *Trioza galii* complex is revised to contain *T. cocquempoti* sp. n., *T. drosopouli* sp. n., *T. galii* Foerster and *T. velutina* Foerster stat. rev., with following new synonymies: *T. rubiae* Baeva and *T. rubicunda* Loginova = *T. galii* and *Trioza distincta* Flor = *T. velutina*, respectively. *T. galii* f. *spinogalii* Šulc and *T. galii* f. *aspinovelutina* Šulc are considered to be of infrasubspecific rank and thus unavailable. *Trioza velutina* var. *thoracica* Flor is an available name regarded as nomen dubium. Lectotypes are designated for *Trioza galii* and *T. velutina*. Adults and last instar larvae (except *T. velutina*) are diagnosed and illustrated. Identification keys are provided. All four species are associated with Rubiaceae on which they induce galls. Confirmed hosts of *T. galii* are *Galium* spp. and *Asperula cynanchica*, literature records also suggest *Sherardia arvensis* and *Rubia* spp. *T. cocquempoti* and *T. drosopouli* develop on *Rubia* spp. *T. velutina* is probably associated with *Galium* spp. but hard evidence is not available. The *T. galii* complex is diagnosed using adult and larval characters. The definition is similar to Conci's (1992) concept of *Spanioza* but excludes *S. tamaninii*. *S. tamaninii* is morphologically intermediate between the *T. galii* complex and the *T. centranthi* complex (associated with Valerianaceae) which may be sister groups. The synonymy of *Spanioza* with *Trioza* is confirmed, and the new combination *Trioza tamaninii* is proposed.

**Keywords:** Hemiptera - Psylloidea - Triozidae - taxonomy - new taxa - Rubiaceae - Palaearctic.

## INTRODUCTION

Species of jumping plant-lice are generally well-defined by their adult and larval morphology as well as their host plants. In particular, the male terminalia are routinely used for species identification. The Palaearctic *Trioza galii* Foerster, as

currently perceived, is a notable exception as the male genital morphology exceeds the usual variability encountered in other *Trioza* species.

Foerster (1848) described both *T. galii* and *T. velutina* from German and Irish localities; some material of *T. galii* was collected on *Galium verum*. The descriptions contain colour and forewing characters but are not diagnostic. Hardy (1853) recorded deformations on *Galium aparine* which he attributed to "*Psylla*" *velutina*. He said that *velutina* appears not to differ from "*Psylla*" *galii*. Flor (1861a), providing detailed descriptions and diagnoses, treated *T. galii* and *T. velutina* as distinct species, pointing out differences in the male paramere. He also assigned a single female specimen from Southern France with a lighter thorax and clear forewing colour, to the variety *Trioza velutina* var. *thoracica*. Again on the basis of a single female, he described *Trioza distincta* from Thuringia, differing from *T. velutina* in the slightly different forewing shape (Flor, 1861b). Flor's more restricted species concept was confirmed by Löw (1882) who examined some of Foerster's and Flor's types. Lethierry (1874), Oshanin (1907) and Aulmann (1913) followed Löw, whereas Scott (1876) and Edwards (1896) adopted Hardy's view, treating *T. galii* and *velutina* as synonyms. Šulc (1913) pointed out that his earlier description (Šulc, 1910) of *T. galii* corresponded with the types of *T. velutina* and having examined types of *T. galii*, *T. velutina* and *T. distincta*, plus other material, reached the same conclusion as Hardy (1853). Thus, he treated *T. velutina*, *T. distincta* and questionably var. *thoracica*, the type of which appears to be lost, as synonyms of *T. galii*. Based on presence or absence of surface spinules as well as colour and shape of the forewing, he defined four forms: *galii* forma typica, f. *spino-galii* Šulc, f. *velutina* and f. *aspinovelutina* Šulc. Boselli (1930) found many specimens in Italy on *Rubia peregrina* which he referred to *Spanioza galii aspinovelutina*. He gave detailed descriptions and illustrations of the adults, larvae and eggs and provided information on their biology. The male paramere of Boselli's material, however, is more massive than those described and illustrated by Šulc (1910, 1913). *T. galii*, in this broad definition, has been reported from all over the Palaearctic, including Japan and Taiwan (Aulmann, 1913; Klimaszewski, 1973; Gegechkori & Loginova, 1990; Ossiannilsson, 1992). According to these authors, the species is associated with *Galium*, *Sherardia* and *Rubia* spp. (Rubiaceae), where it induces characteristic deformations on the buds, shoots and leaves, which can be above or below ground (e.g. Houard, 1909; Docters van Leeuwen, 1937).

Adults are regularly encountered by sweeping herbaceous vegetation, although rarely on the host plants. Larval material, by contrast, is generally difficult to find. The first larval description referred to *T. galii* is by Kieffer (1889) who examined material from *Sherardia arvensis* but his description is not diagnostic. The dorsum of the larva is said to be dark brown. A more detailed larval description referred to *T. galii* is that by Boselli (1930). White & Hodkinson (1981) used Boselli's description in their handbook of the British species, and Ossiannilsson (1992) in the Fauna Scandinavica described Italian rather than Scandinavian specimens.

Three additional Palaearctic species are reported from Rubiaceae. Baeva (1972) described *Trioza rubiae* from Turkmenia based on a single series collected on *Rubia florida*, which she related to *Trioza foersteri* Meyer-Dür and *Trioza rotundata* Flor. Loginova (1978) added *Trioza rubicunda*, again based on a single series, collected in

Kazakhstan on *Galium* sp. According to Loginova *T. rubicunda* is closest to *T. galii* f. *velutina* from which it differs in the reduced surface spinules and a broader paramere. *T. rubiae* and *T. rubicunda* have not been subsequently reported. Conci (1992) described *Spanioza tamaninii* from Italian and Slovakian specimens, one of which was collected on *Galium anisophyllum*. He suggested that *S. tamaninii* is closely related to *galii* and that its host may be *Galium*.

*Trioza galii* was selected by Enderlein (1926) as type species of *Spanioza*, a genus which he erected for triozids with a short Rs vein in the forewing. The artificial nature of this concept was pointed out by Tuthill (1943) who synonymised it with *Trioza*. Conci (1992) considered *Spanioza* a valid genus and redefined it to include *Trioza galii* and its "formae", *Trioza rubiae* Baeva, *Trioza rubicunda* Loginova and *Spanioza tamaninii* Conci. This was not followed by Burckhardt & Couturier (1994) who treated the *Trioza galii* group as part of the large artificial genus *Trioza*.

Over the last few years collections from the Mediterranean as well as Central and Western Europe yielded material including larvae and host records which permit a re-evaluation of the taxonomy of the *Trioza galii* complex. Wagner & Franz (1961) suggested that *T. galii* in the broad definition by Šulc (1913) is a species complex, and Conci (1992) wrote that *Trioza galii* and its "formae" require revision. The present paper provides this revision and re-examines the validity of *Spanioza*.

## MATERIAL AND METHODS

Material has been examined or is mentioned from following institutions:

BMNH	Natural History Museum, London
DEZA	Dipartimento di Entomologia e Zoologia Agraria dell'Università, Portici
EAUT	Institute of Zoology and Botany, Estonian Agricultural University, Tartu
MHNG	Muséum d'histoire naturelle, Geneva
MMBC	Moravské Muzeum, Brno
MNHN	Muséum national d'histoire naturelle, Paris
NHMB	Naturhistorisches Museum, Basel
NHNV	Naturhistorisches Museum, Vienna
SMTD	Staatliches Museum für Tierkunde, Dresden
ZISP	Zoological Institute, St. Petersburg
ZMHB	Museum für Naturkunde der Humboldt-Universität, Berlin
ZSSM	Zoologische Staatssammlung, Munich.

The morphological terminology mainly follows Ossiannilsson (1992). Drawings were prepared from cleared specimens mounted permanently in Euparal or Canada Balsam or temporarily in glycerine. Measurements were taken from slide mounted specimens, except for the total body length which is taken from dry mounted specimens measured from the apex of head to the apex of forewing when folded over the body.

## RESULTS

The *Trioza galii* Foerster, 1848 species complex

### DESCRIPTION

Adult. Coloration mostly dark brown to black, in *T. cocquempoti* and *T. drosopouli* thorax yellowish, brown or dark dorsally, sometimes with longitudinal

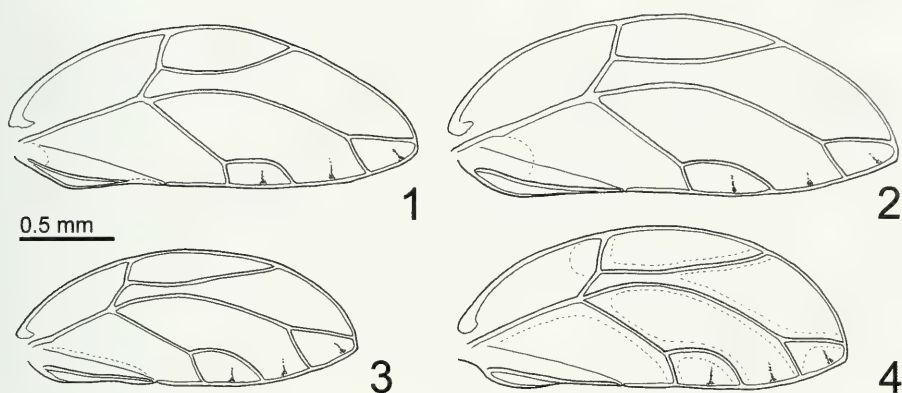


stripes; area around wing insertion yellowish or brown; intersegmental membranes reddish; antennal segment 3, tibiae and tarsi whitish. Forewing almost colourless or with yellowish or light brown tinge; veins yellowish or light brown, vein C+Sc often brown or dark brown in basal part. Young specimens lighter.

Head slightly narrower than mesonotum, weakly inclined from longitudinal body axis, at a 45° angle. Vertex shiny, weakly produced anteriorly on either side of mid-line. Genal processes variable in size and shape, conical, subacute, ranging from one to two thirds vertex length. Antenna 10-segmented, segment 3 longer than segments 4 and 5 together; segment 10 bearing one long and one very short terminal seta respectively (Fig. 21). Clypeus short, pyriform. Thorax weakly curved dorsally. Metacoxa with horn-shaped, subacute meracanthus; metatibia weakly widened basally and apically, with some minute basal spines and 1+3 sclerotised apical spurs; metatarsus without sclerotised spurs. Forewing (Figs 1-4) transparent, variable in size, shape and colour, elongate, strongly pointed, angular or bluntly angular apically; vein Rs short, bifurcation of vein M slightly or strongly distal to line linking apices of veins Rs and Cu<sub>1a</sub>. Wing membrane transparent; apart from wing base usually lacking surface spinules, with the exception of *T. velutina* where spinules are always present, forming more or less extended fields. Radular spinules forming narrow stripes in cells m<sub>1</sub>, m<sub>2</sub>, and cu<sub>1</sub>. Hindwing membranous, about two thirds forewing length. Costal setae ungrouped; R+M+Cu<sub>1</sub> indistinctly trifurcating. Abdominal tergite 3 (and occasionally 4) in male and tergite 4 (and occasionally 5) in female bearing a row of lateral setae. Male proctiger (Figs 5, 8, 11, 16) 1-segmented, weakly produced or lobed posteriorly, covered in moderately long setae apically and posteriorly. Subgenital plate subglobular, with a few long setae laterally and ventrally. Paramere (Figs 6, 9, 12, 13, 17) shorter than proctiger, massive or lamellar; sparsely covered in long setae on outer face apically and along hind margin; inner face covered in long thin setae mainly basally, apically and along hind margin, with a group of shorter, stout setae along fore margin in basal half. Proximal portion of aedeagus strongly curved at base, almost straight apically; distal portion (Figs 7, 10, 14, 15, 18) relatively short with large apical dilatation which varies from almost rectangular to distinctly hooked. Sclerotised end tube of ductus ejaculatorius short, weakly curved. Female proctiger (Figs 23-26) short with relatively large circumanal ring. Subgenital plate short.

Fifth instar larva (Fig. 28). Coloration varying from uniformly yellow or light ochreous to yellow with more or less extended pattern on head, thorax, wing buds and abdomen to completely dark. Body oval, bearing a single row of densely spaced, lateral truncate setae. Antenna 6-segmented. Head broadly rounded anteriorly. Legs with short claws and small, fan-shaped tarsal arolium. Humeral lobes blunt, relatively short. Circumanal ring small, with a single row of pores. Dorsum of body lacking macroscopic setosity. Tarsal arolium transversely oval, lacking pedicel, with unguitractor (Figs 29-31). Claws relatively small.

Egg. Spindle-shaped, longer than three times its width, with short basal pedicel and no apical filament. The egg is laid perpendicularly on the leaf margins.



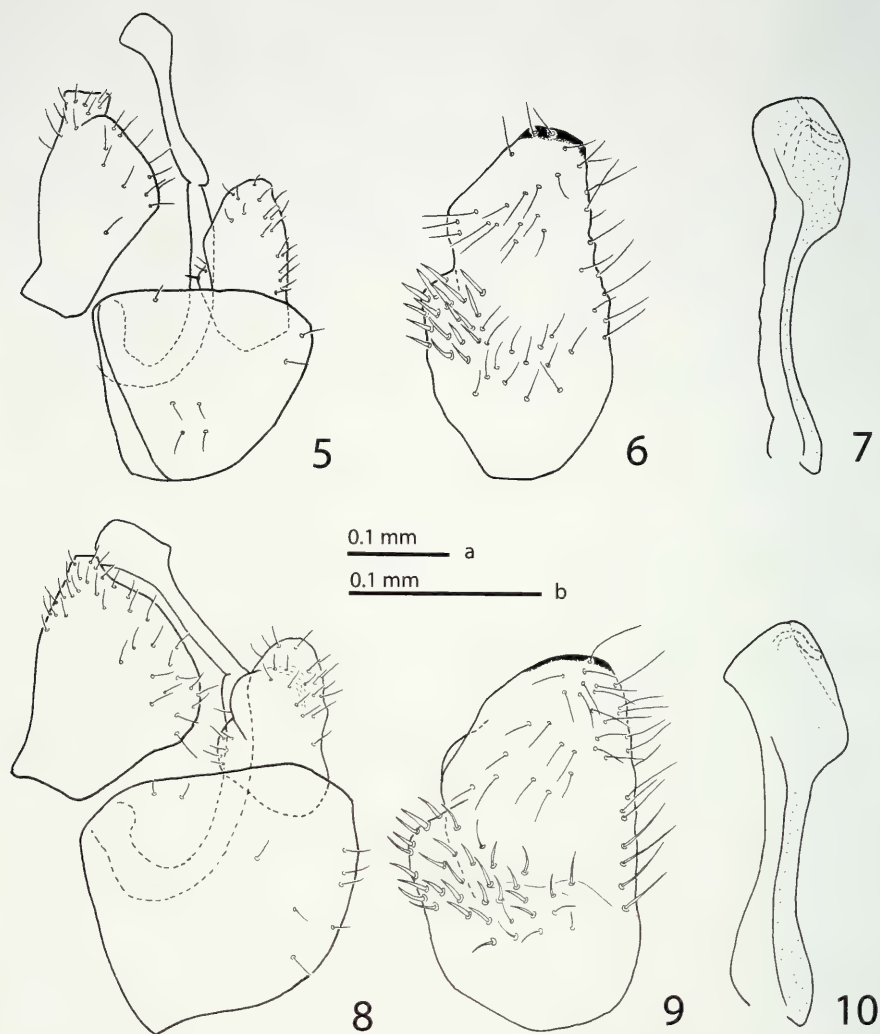
FIGS 1-4

Forewing of *Trioza* spp. 1 – *T. cocquempoti*; 2 – *T. drosopouli*; 3 – *T. galii*; 4 – *T. velutina*.

## DISCUSSION

The *T. galii* complex, as defined above, constitutes a small, probably monophyletic group within the large artificial genus *Trioza*. It is restricted to the Palaearctic. It may be most closely related to the *T. centranthi* complex (*T. centranthi* (Vallot), *Trioza nana* Gegechkori and *T. valerianae* Gegechkori), associated with Valerianaceae. Adult *T. galii* and *T. velutina* resemble *T. centranthi* (Vallot) in morphology, size and colour. The distribution of surface spinules on the forewing is variable in *T. centranthi*. They may form relatively extended fields in all cells except for  $c+sc$  or they may be restricted to cell  $cu_2$ . In *T. centranthi* vein  $Rs$  of the forewing tends to be relatively long and sinuous, and the bifurcation of vein  $M$  lies near the line joining the apices of veins  $Rs$  and  $Cu_{1a}$ ; in *T. galii* and *T. velutina* in contrast vein  $Rs$  is shorter and almost straight or concave; the bifurcation of vein  $M$  is more distant to the line joining the apices of veins  $Rs$  and  $Cu_{1a}$ . *T. centranthi* bears terminal setae on antennal segment 10, with the shorter seta about half as long as the longer one (Fig. 22), in the *T. galii* complex the shorter seta is only about a quarter to a third as long as the longer (Fig. 21). The *T. centranthi* complex is characterised by the irregularly triangular paramere, which sometimes bears a large antero-apical lobe (absent in the *T. galii* complex), and by the apical dilatation of the distal portion of the aedeagus, which bears small lateral spines (*T. centranthi*, Fig. 20) (absent in the *T. galii* complex, Figs 7, 10, 14, 15, 18). The female subgenital plate of *T. centranthi* (Fig. 27) has, on either side, a group of long setae near the dorsal margin, which are longer than the other hairs (hairs laterally, ventrally and terminally are of about the same length in the *T. galii* complex, Figs 23-26).

The present concept of the *T. galii* complex differs in two major details from that of Conci (1992). In addition to *T. galii*, *T. rubiae* and *T. rubicunda*, Conci included *Spanioza tamaninii* in the group. *S. tamaninii* has so far been recorded from a few specimens from Italy and Slovakia only. It differs from the *T. galii* complex and the *T. centranthi* complex in having antennae which have light segments 3-8 rather than dark segments with a strongly contrasting light segment 3. The paramere shape, the termi-

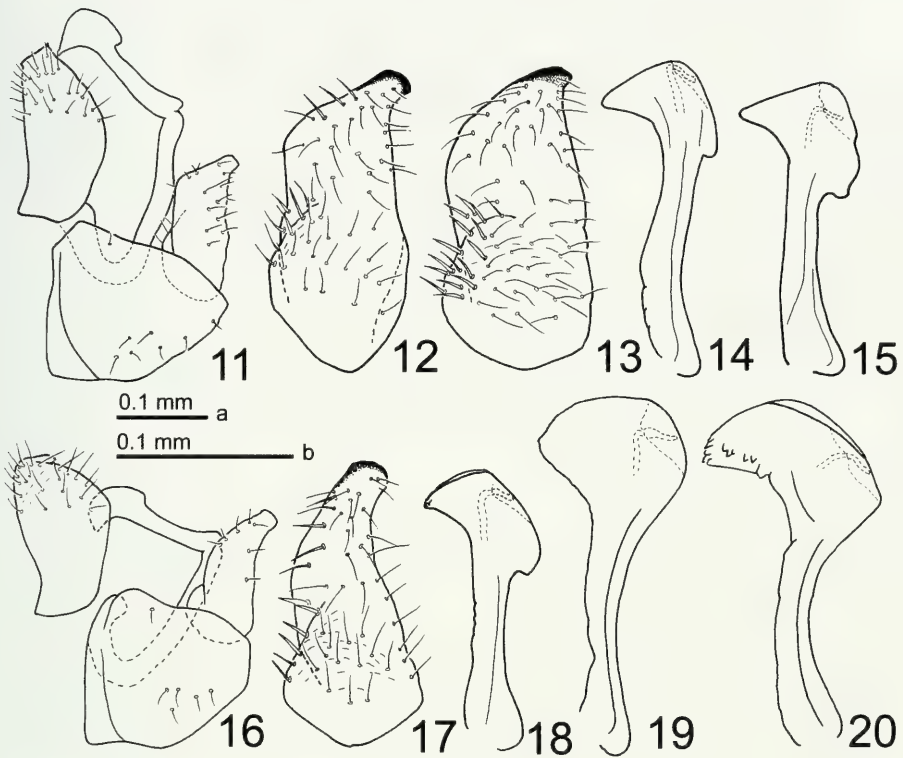


FIGS 5-10

Male genital structures of *Trioza* spp. 5-7 - *T. cocquempoti*; 8-10 - *T. drosopouli*. 5, 8 - Terminalia, in profile, scale a; 6, 9 - paramere, inner surface, scale b; 7, 10 - distal portion of aedeagus, scale b.

nal antennal setae and probably also the lateral setosity on the female subgenital plate are as in species of the *T. centranthi* complex. Apart from the antennal colour *S. tamaninii* differs from the *T. centranthi* complex in the apex of the aedeagus (Fig. 19) lacking lateral spines (cf. Fig. 20 for *T. centranthi*). Incidentally Conci's drawing of the aedeagus appears to be artefactual. Larval material is necessary to determine the phylogenetic relationship of *S. tamaninii*.





FIGS 11-20

Male genital structures of *Trioza* spp. 11-15 – *T. galii*; 16-18 – *T. velutina*; 19 – *T. tamaninii*; 20 – *T. centranthi*. 11, 16 – Terminalia, in profile, scale a; 12, 13, 17 – paramere, inner surface, scale a; 14, 15, 18-20 – distal portion of aedeagus, scale b.

Conci (1992) resurrected the genus *Spanioza* for the *T. galii* complex and *S. tamaninii*. He neither provided convincing autapomorphies for *Spanioza* nor did he define a sister group. This makes his *Spanioza* highly artificial and without phylogenetic significance. We follow Burckhardt & Couturier (1994) who treated *Spanioza* as a synonym of *Trioza*. Here we formally transfer *Spanioza tamaninii* to *Trioza* as *T. tamaninii* (Conci) comb. n.

## TAXONOMIC TREATMENT

Key for the identification of the species of the *Trioza galii* complex

### Adults

- 1 Antenna longer than 1.1 mm. Male proctiger strongly produced posteriorly (Figs 5, 8). Paramere (Figs 6, 9) massive, blunt apically. Apex of distal portion of aedeagus subrectangular or reniform (Figs 7, 10). Ventral and posterior margin of female subgenital plate, in profile (in cleared specimens), forming an angle  $> 90^\circ$  (Figs 23, 24) . . . . . 2

- Antenna shorter than 1.1 mm. Male proctiger tubular, weakly produced posteriorly (Figs 11, 16). Paramere (Figs 12, 13, 17) slender, with apical digitiform process. Apex of distal portion of aedeagus hooked (Figs 14, 15, 18). Ventral and posterior margin of female subgenital plate, in profile (in cleared specimens), forming an angle  $< 90^\circ$  (Figs 25, 26) . . . . . 3
- 2 Male proctiger with narrow posterior lobe (Fig. 5). Paramere (Fig. 6), in profile, with narrow angular bulge above the middle along the fore margin; apex angular. Distal portion of aedeagus (Fig. 7) with reniform apical dilatation. Female terminalia as in Fig. 23. Algeria, France, Italy, Morocco, Spain . . . . . *T. cocquempoti* sp. n.
- Male proctiger with large posterior lobe (Fig. 8). Paramere (Fig. 9), in profile, with broad bulge in apical third along the fore margin; apex broadly rounded. Distal portion of aedeagus (Fig. 10) with subrectangular apical dilatation. Female terminalia as in Fig. 24. Greece . . . . . *T. drosopouli* sp. n.
- 3 Forewing (Fig. 3) membrane lacking surface spinules except for base of cell  $cu_2$ . Paramere robust, fore margin irregularly curved in apical half (Figs 12, 13). Apex of distal portion of aedeagus with large apical hook (Figs 14, 15). Female proctiger with relatively long and slender apical process, subgenital plate, in profile, truncate apically (Fig. 25) . . . . . *T. galii*
- Forewing (Fig. 4) membrane with surface spinules present in all cells forming more or less extended fields. Paramere slender, evenly curved (Fig. 17). Apex of distal portion of aedeagus with relatively short apical hook (Fig. 18). Female proctiger with relatively short massive apical process, subgenital plate, in profile, bearing a small point apically (Fig. 26) . . . . . *T. velutina*

#### Fifth instar larvae

(larvae of *T. velutina* unknown)

- 1 Body dimensions small, body length  $< 1.8$  mm, see also table 2 . . . . . *T. galii*
- Body dimensions large, body length  $> 1.8$  mm, see also table 2 . . . . . 2
- 2 Marginal sectasetae on forewing pads over 100, and on hindwing pads over 15. West Mediterranean . . . . . *T. cocquempoti* sp. n.
- Marginal sectasetae on forewing pads less than 100, and on hindwing pads less than 15. Greece . . . . . *T. drosopouli* sp. n.

#### *Trioza cocquempoti* sp. n.

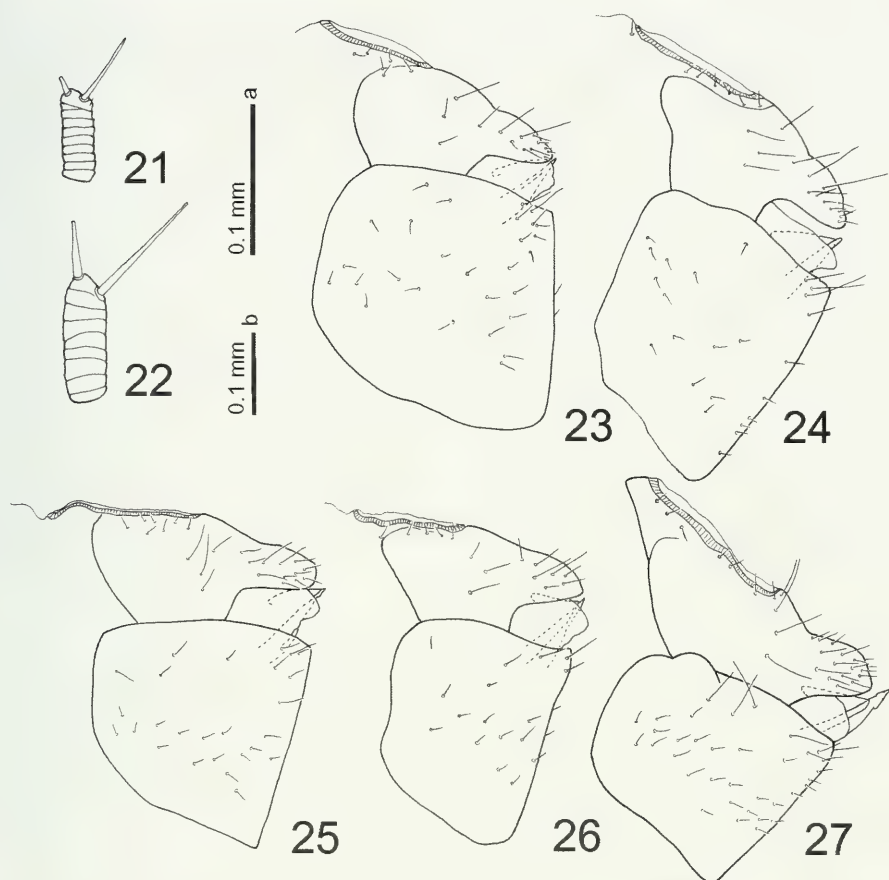
Figs 1, 5-7, 23, 29

*Spanioza galii aspinovelutina* sensu Boselli, 1930: 14, nec Šulc, 1913.

*Trioza galii* sensu White & Hodkinson, 1982: 43, nec Foerster, 1848.

MATERIAL EXAMINED: Holotype ♂, **France**: Gard, 5 km W Pont-St.-Esprit, 22.x.1988, *Galium* sp. (D. Burckhardt) (MHNG, dry mounted).

Paratypes. **Algeria**: 1 ♀, Atlas of Blida Chr  a, Les Glaci  res, 1100 m, 3.v.1988 (D. Burckhardt) (MHNG, dry mounted); 1 ♀, Grande Kabylie, Oued Isser, bridge N24, 21.v.1988 (D. Burckhardt) (MHNG, dry mounted). - **France**: 2 ♀, Corsica, Luri, Col de Sainte Lucie, 24.iv.1992 (W. Della Giustina) (NHMB, dry mounted); 1 ♀, Gard, same data as holotype; 1 ♂, 1 ♀, Var, Roquebrune-sur-Argens, Les Sauterons, 15-20.iv.1990 (C. Lienhard) (NHMB, dry mounted); 1 ♂, 2 ♀, Indre et Loire, La Roche-Clermout, Malaise trap, 11.viii.1989 (C.



FIGS 21-27

*Trioza* spp. 21, 25 – *T. galii*; 22, 27 – *T. centranthi*; 23 – *T. cocquempoti*; 24 – *T. drosopouli*; 26 – *T. velutina*. 21, 22 – Antennal segment 10, scale a; 23-27 – female terminalia, in profile, scale b.

Cocquempot) (MMBC, dry mounted and stored in glycerine); 1 ♂, Indre et Loire, Roquebrunne-sur-Argens, 15-20.iv.1990 (C. Cocquempot) (MMBC, stored in glycerine); 2 ♀, Tarn, Albi, Fargues, 30.v.1933, *Crataegus* (A. Perrier) (MNHN, dry mounted); 1 ♀, Tarn, Albi, 7.vi., *Crataegus* (A. Perrier) (MNHN, dry mounted); 1 ♀, Albi, Castelnau-de-Lévi, 8.iv., *Rhus* (A. Perrier) (MNHN, dry mounted); 1 ♀, Albi, Creysence, 14.vi., *Buxus* (A. Perrier) (MNHN, dry mounted); 1 ♂, Vaucluse, La Roque-Alric, near Beaumes-de-Venise, 300 m, 23.iv.1984 (C. Lienhard) (MHNG, slide mounted); 2 ♂, Vaucluse, near Vacqueyras, river Ouvèze, 60 m, 26.iv.1984 (C. Lienhard) (MHNG, dry mounted); 6 ♂, 7 ♀, without locality data (MNHN, dry mounted). - **Italy**: 1 ♂, 5 ♀, 2 parasitised larvae, Portici, 25.v.1928, *Rubia* (F. B. Boselli) (DEZA, dry mounted); ca. 100 larvae and exuviae, 21.v.1928, *Rubia* (F. B. Boselli) (DEZA, alcohol); 10 ♂, 9 ♀, 45 larvae and exuviae, Portici, Parco Gussone, v-vi.2004 (P. A. Pedata) (DEZA, alcohol; NHMB, slide mounted); 1 ♂, Basilicata, Potenza, PR Gallipoli Cognato, near Monte Crocchia, 810-910 m, 1-4.v.2001, Malaise trap 2 (Springate *et al.*) (DEZA, alcohol); 1 ♂, Basilicata, Matera, PR Gravina di Matera, 15 km E of Masseria San Francesco, 16-19.iii.2002,



290-310 m, Malaise trap (Springate *et al.*) (DEZA, alcohol); 2 ♀, same but 27-30.iv.2001, 290-370 m; 2 ♂, 2 ♀, same but PR Gravina di Matera, 2.5 km W of road to Ginosa, 28-30.iv.2001; 1 ♀, same but PR Gravina di Matera, 1.5 km W of road to Ginosa, 25-28.ix.2001; 1 ♂, Campania, Napoli, Parco Gussone, 55 m, 1-4.iv.2002, Malaise trap (Springate *et al.*) (DEZA, MMBC, NHMB, alcohol, dry mounted); 2 ♂, 4 ♀, same but 55-80 m, 17-20.v.2001; 3 ♀, same but Caserta, WWF San Silvestro, 270-300 m, 13-16.v. 2001. - **Morocco**: 1 ♀ without wings, Tanger (MMBC, Šulc collection). - **Spain**: 1 ♂, Zaragoza Province, Monegros Region, Pina de Ebro, 360 m, 2.vi.1990 (J. Blasco-Zumeta) (MHNG, dry mounted).

Material excluded from type series. **France**: 1 adult without abdomen, Vaucluse, La Roque-Alric, 350 m, 27.iv.1984 (C. Lienhard) (MHNG, dry mounted).

**DIAGNOSIS**: Adult. Total body length 2.8-3.3 mm. Colour of thorax yellow, sometimes brown or dark brown dorsally, or with brown longitudinal stripes on mesopraescutum and mesoscutum. Genal processes 0.6 times as long as vertex along midline, subacute apically. Forewing (Fig. 1) elongate, pointed apically; bifurcation of vein M distinctly distal to line connecting apices of veins Rs and Cu<sub>1a</sub>. Forewing membrane lacking surface spinules except at wing base. Hindwing two thirds of forewing length. Male proctiger (Fig. 5) relatively massive, strongly produced posteriorly. Paramere (Fig. 6) massive, truncate apically, in profile, with narrow angular bulge in apical third along the fore margin; apex angular. Distal portion of aedeagus (Fig. 7) with reniform apical dilatation. Female proctiger (Fig. 23) relatively short, pointed apically; ventral and posterior margin of female subgenital plate, in profile (in cleared specimens), forming an angle > 90°. Measurements as in Table 1.

Fifth instar larva described by Boselli (1930) as *Spanioza galii aspinovelutina*. With following numbers of marginal setae (one side only): head 42-46, forewing pad 109-113, hindwing pad 15-18, caudal plate 108-122. Tarsal arolium transversely oval (Fig. 29). Measurements as in Table 2.

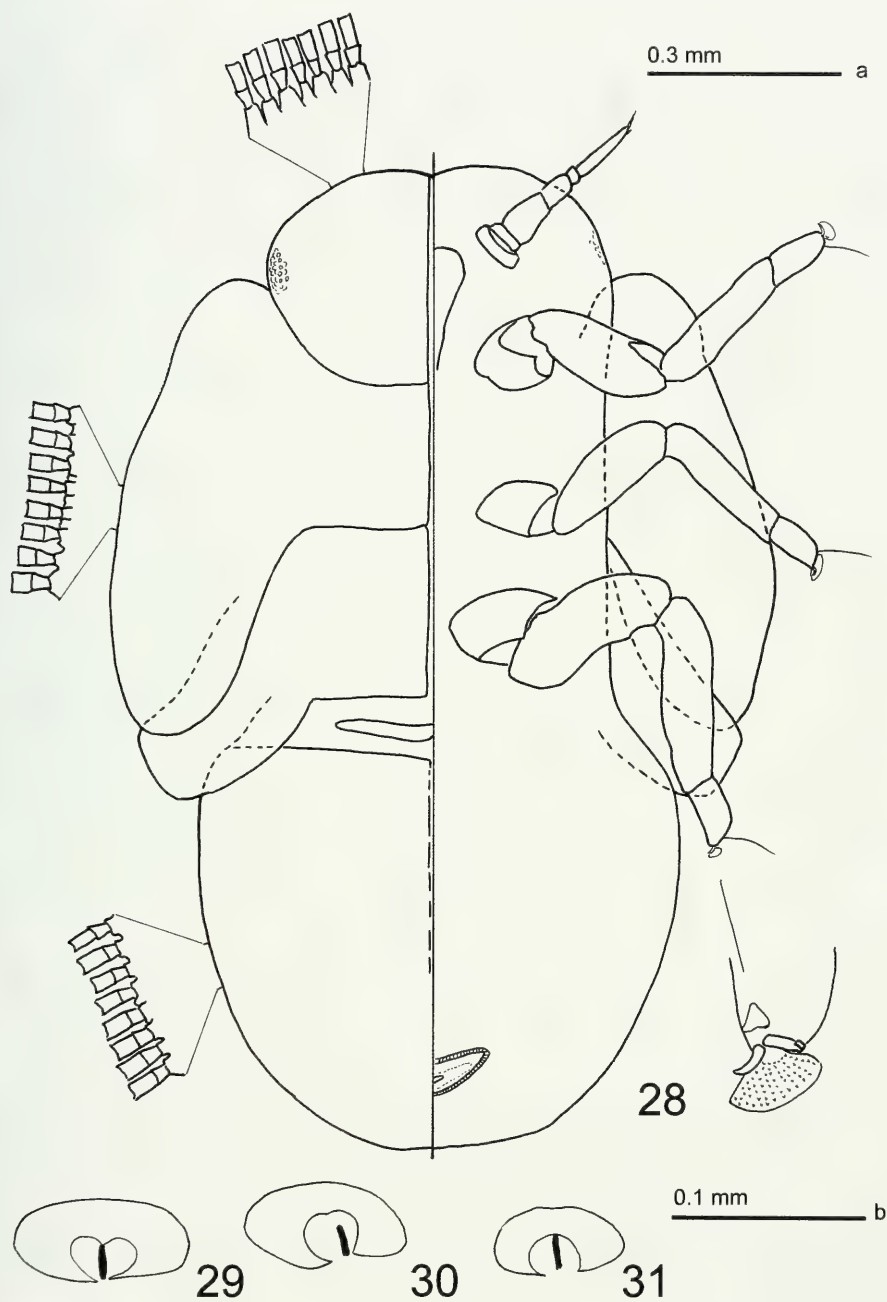
**ETYMOLOGY**: The species is dedicated to Christian Cocquempot, one of the collectors of the new species.

**DISTRIBUTION**: Algeria, France, Italy, Morocco, Spain.

**BIOLOGY**. Host plant. Boselli (1930) collected eggs, larvae and adults exclusively on *Rubia peregrina*. The larvae induce a strong curling of the leaves. Boselli could not find any specimens on *Galium*. The holotype ♂ and a female paratype from France have been taken on *Galium* sp. but no larvae were found. At the moment there is no evidence that *Galium* is a host plant.

According to Boselli (1930) larvae of *T. cocquempoti* aestivate and hibernate in the galls on the host, which also has a summer and winter dormancy. In spring and autumn when the host produces new flush, the adults emerge and, a few days later after copulation, the females lay their eggs. The eggs are laid perpendicularly on the leaf margins or stems. Depending on the season the egg development takes two (spring generation) to over four weeks (autumn generation). If the conditions in spring are particularly favorable, three generations per year are possible.

**COMMENTS**: The description of *Spanioza galii aspinovelutina* by Boselli (1930) concerns *T. cocquempoti*, which was also confirmed by the examination of Boselli's material. For the validity of the name *aspinovelutina* see comments to *T. galii*. The larval description by White & Hodkinson (1982), tentatively referred to *T. galii*, is based on Boselli's (1930) description and, hence, refers to *T. cocquempoti*.



FIGS 28-31

*Trioza* spp. 28, 31 – *T. galii*; 29 – *T. cocquempoti*; 30 – *T. drosopouli*. 28 – Last instar larva, left dorsal face, right ventral face (scale a), with details of marginal setasetae and tarsal apex (scale b); 29-31 – tarsal arolium, scale b.

*Trioza drosopouli* sp. n.

Figs 2, 8-10, 24, 30

MATERIAL EXAMINED: Holotype ♂, **Greece**: Attiki, Tatoi, NW Athens, 250 m, 1.v.1995, *Rubia tinctorum* (P. Lauterer) (NHMB, dry mounted).

Paratypes. **Greece**: 16 ♂, 43 ♀, 1 exuvia, Attiki, same data as holotype (MMBC, 14 ♂, 38 ♀ dry mounted, 1 ♂, 2 ♀, 1 exuvia, stored in glycerine; NHMB, 2 ♀ ♀ dry mounted, 1 ♂, 1 ♀ stored in glycerine); 4 ♂, 12 ♀, same data but 200 m, 7.v.1995, clearing and *Pinus* wood (MMBC, 3 ♂, 11 ♀ dry mounted; NHMB, 1 ♂, slide mounted, 1 ♀ dry mounted); 2 ♂, 3 ♀, Attiki, Paríntha Mountains, Agía Trías Parínthos, 1200 m, 28.v.1995, *Rubia tinctorum* in wood undergrowth (P. Lauterer) (MMBC, 1 ♂, 2 ♀ dry mounted; NHMB, 1 ♂, 1 ♀ dry mounted); 1 ♀, Akarnanía, Gavrolimni, 120 m, 17.iii.1982 (C. Lienhard) (MHNG, dry mounted); 1 ♀, Arkadia, E Peloponnissos, 4 km E of Agios Petros, 900 m, 5.v.1995 (P. Lauterer) (MMBC, dry mounted); 1 exuvia, Messinía, Messene, between Kalamata and Pilos, 16.v.1979 (D. Burckhardt) (MHNG, slide mounted).

Material not included in type series. **Greece**: 1 ♂, 11 ♀, damaged, Attiki, same data as holotype (MMBC); 1 very teneral ♀, Messinía, Messene, between Kalamata and Pilos, 16.v.1979 (D. Burckhardt) (MHNG, slide mounted).

DIAGNOSIS: Adult. Total body length 2.8-3.4 mm. Colour of thorax yellow or ochreous; mesopraescutum dark brown or black, sometimes with a median longitudinal lighter stripe; mesoscutum ochreous to light brown, sometimes with dark brown longitudinal stripes, generally lighter than mesopraescutum. Genal processes 0.8 times as long as vertex along mid-line, subacute apically. Forewing (Fig. 2) elongate, pointed apically; bifurcation of vein M distinctly distal to line connecting apices of veins Rs and Cu<sub>1a</sub>. Forewing membrane lacking surface spinules except at wing base. Hindwing two thirds of forewing length. Male proctiger (Fig. 8) massive, strongly produced posteriorly. Paramere (Fig. 9) massive, blunt apically, in profile, with large angular bulge in apical third along the fore margin; apex rounded. Distal portion of aedeagus (Fig. 10) with angular apical dilatation. Female proctiger (Fig. 24) relatively short, pointed apically; ventral and posterior margin of female subgenital plate, in profile (in cleared specimens), forming an angle > 90°. Measurements as in Table 1.

Fifth instar larva. With following numbers of marginal setae (one side only): head 39-44, forewing pad 94-99, hindwing pad 11-12, caudal plate 97-110. Tarsal arolium oval (Fig. 30). Measurements as in Table 2.

ETYMOLOGY: The species is dedicated to our friend Sakis Drosopoulos who organised the collecting trip of Pavel Lauterer to Greece and assisted in the field.

DISTRIBUTION: Greece (Akarnanía, Arkadia, Attiki, Messinía).

BIOLOGY: A larval skin and adults, including teneral specimens, have been collected on *Rubia tinctorum* which is a likely host. A few teneral adults were collected on 1 May and followed by mature adults up to 28 May, suggesting that the bionomics may be similar to that of *T. cocquempoti*.

COMMENTS: No reliable characters could be found for separating the females of *T. drosopouli* and *T. cocquempoti*.

*Trioza galii* Foerster

Figs 3, 11-15, 21, 25, 28, 31

*Trioza galii* Foerster, 1848: 87; Šulc, 1913: 38, p. p. Lectotype ♂, **Germany**: Nordrhein-Westfalen, near Aachen (A. Foerster) (MMBC), here designated, examined.  
*Psylla galii*; Hardy, 1853: 3876.



*Trioza galii* Foerster f. *aspinovelutina* Šulc, 1913: 44. Name unavailable, articles 45.6.1 and 45.6.4, ICZN, 1999.

*Spanioza galii*; Enderlein, 1926: 400; Conci, 1992: 258.

*Trioza rubiae* Baeva, 1972: 63. Holotype ♂, **Turkmenistan**: north-western part of Turkmen-Khorasan Mountains, around Yaradzha, 21.iv.1971, *Rubia florida* (V. Baeva, O. Rudenko) (ZISP, dry mounted), examined. **Syn. n.**

*Trioza rubicunda* Loginova, 1978: 111. Holotype ♂, **Kazakhstan**: Chimkent District, Aksu-Dzhibagly Reservation, Talass Mountain Range, 80 km E Chimkent, 10.vi.1966, *Galium* sp., (M. M. Loginova) (ZISP, dry mounted), examined. **Syn. n.**

*Spanioza rubiae*; Conci, 1992: 258.

*Spanioza rubicunda*; Conci, 1992: 258.

**MATERIAL EXAMINED:** Material was examined from following countries: Algeria; Armenia; Austria: Oberösterreich, Steiermark; Bulgaria; Czech Republic, Bohemia, Moravia; Cyprus; France: Finistère, Haute-Garonne, Hautes-Pyrénées, Hérault, Indre et Loire, Landes, Maine-et-Loire, Nord, Pas-de-Calais, Tarn, Var; Germany: Baden-Württemberg, Berlin, Brandenburg, Hessen (including paralectotype ♂, Ems, leg. C.H.G. von Heyden), Nordrhein-Westfalen (including ♂ lectotype and paralectotypes 6 ♂ and 1 adult without abdomen, Aachen), Sachsen; Greece: Atikí, Corfu, Crete, Cyclades, Évia; Israel; Italy: Alto Adige, Puglia; Jordan; Kazakhstan (including ♂ holotype of *Trioza rubicunda*); Kyrgyzstan; Malta; Slovakia; Slovenia; Spain: Caceres, Zaragoza, Canaries; Switzerland: Aargau, Basel-Land, Genève, Luzern, Neuchâtel, Vaud, Valais; Turkey: Aydin; Tunisia; Turkmenistan (including ♂ holotype of *Trioza rubiae*); United Kingdom: England, Scotland, Wales (BMNH, MHNG, MMBC, MNHN, NHMB, NHMV, SMTD, ZISP, ZMHB, ZSSM).

**DIAGNOSIS:** Adult. Total body length 2.3-3.2 mm. Colour of thorax usually dark brown or almost black with exception of area around wing insertion which is yellowish. Younger specimens with light colour more expanded and dark areas brown rather than black. Genal processes 0.3-0.7 times as long as vertex along mid-line, blunt to subacute apically. Forewing (Fig. 3) varying from relatively short and wide to elongate, angular apically; bifurcation of vein M on or slightly distal to line connecting apices of veins Rs and Cu<sub>1a</sub>. Forewing membrane lacking surface spinules except at wing base. Hindwing three quarters or four fifth of forewing length. Male proctiger (Fig. 11) relatively slender, weakly produced posteriorly. Paramere (Figs 12, 13) lamellar, with an antero-basal bulge and subparallel margins in the middle third, apical third abruptly narrowed to posteriorly directed apex. Distal portion of aedeagus (Figs 14, 15) with large hook-shaped apical dilatation. Female proctiger (Fig. 25) with relatively short thick apical process; subgenital plate, in profile, bearing small point apically. Measurements as in Table 1.

Fifth instar larva (Fig. 28). With following numbers of marginal setae (one side only): head 34-37, forewing pad 88-110, hindwing pad 11-12, caudal plate 98-101. Tarsal arolium oval (Fig. 31). Measurements as in Table 2.

**DISTRIBUTION:** *T. galii* is widely distributed in the West Palaearctic and Central Asia. We have not seen any specimens from the East Palaearctic where the species probably also occurs. It has been reported from all over the Palaearctic including Japan and Taiwan (Aulmann, 1913; Klimaszewski, 1973; Gegechkori & Loginova, 1990; Ossiannilsson, 1992) but some of the records may concern other species of the *T. galii* complex.

**BIOLOGY:** *T. galii* is reported to form galls on the buds, stems and leaves of *Galium*, *Rubia* and *Sherardia* spp. We have examined larvae and galls on following



plants: *Galium album*, *G. aparine*, *G. palustre* and *Asperula cynanchica*. The species overwinters as adult. The adults of the new generation appear in June or July. With the available information it is impossible to deduce the number of yearly generations of *T. galii*.

COMMENTS: The type series of *Trioza galii*, originally deposited in the NHMV and now in the MMBC, contains one series from Aachen and one from Ems, leg. von Heyden. The former is homogeneous, but the latter is mixed, including 1 ♂ of *T. galii* and 3 ♂ of *T. velutina*. As Foerster's (1848) description of *T. galii* is not diagnostic, and for stabilising the nomenclature, a lectotype is selected from the series from Aachen. This accords with Flor's (1861a) and Löw's (1882) concept of *T. galii*.

Šulc (1913) admitted that *Trioza galii* in his broad definition, which included *T. distincta* and *T. velutina* as synonyms, exhibited a surprisingly large variation in size and shape of the genal processes, in body and forewing colour, in forewing shape, venation and spinulation as well as in genital morphology. He interpreted differences in the male terminalia mostly as artefacts. For the other characters he suggested that extremes are linked by intermediates. Based on forewing characters he subdivided *T. galii* into four forms for two of which he introduced the names f. *spinogalii* and f. *aspinovelutina*, in addition to *galii* forma typica and f. *velutina*. According to paragraph 45.6.4 of the ICZN (1999) a name introduced before 1961 as "variety" or "form" has to be considered subspecific, unless its author also expressly gave it infrasubspecific rank, or the content of the work unambiguously reveals that the name was proposed for an infrasubspecific entity, in which case it is infrasubspecific. The latter applies to the two names as Šulc mentioned that these narrowly defined forms are linked by intermediates and, thus, implying that they are artificial groupings for convenience rather than diagnosable entities such as subspecies or species. As infrasubspecific names they are not available. Boselli (1930) used the name *Spanioza galii apinovelutina* for Italian specimens of *T. cocquempoti*, thus misinterpreting Šulc's taxon, which represents *T. galii* judging from Šulc's figures of Austrian specimens. Boselli did not raise the name *spinogalii* to subspecies or species rank, and the name does not become available through Boselli (1930).

The examination of the male holotypes of *T. rubiae* and *T. rubicunda* showed that they are conspecific with *T. galii*, with which they are synonymised.

In *Trioza chenopodii* Reuter the forewing shape is variable as in *T. galii*. Lauterer (1982) demonstrated for the former, that this variation is seasonal, induced by day length. We found no evidence in species of the *T. galii* complex for seasonal differences as in *T. chenopodii*.

***Trioza velutina* Foerster, stat. rev.**

Figs 4, 16-18, 26

*Trioza velutina* Foerster, 1848: 87. Lectotype ♂, Germany: Rheinland-Pfalz, near Boppard (A. Foerster) (MMBC), here designated, examined.

*Psylla velutina*; Hardy, 1853: 3876.

*Trioza distincta* Flor, 1861b: 401. Holotype ♀, Germany: Thüringen, Ruhla, mid June (G. Flor) (MMBC), examined. **Syn. n.**

*Trioza galii* sensu Šulc, 1910: 16, nec Foerster, 1848; Šulc, 1913: 45. Misidentification.

*Trioza galii*, Šulc, 1913: 38, p. p.

*Trioza galii* Foerster f. *spinogalii* Šulc, 1913: 44. Name unavailable, articles 45.6.1 and 45.6.4, ICZN, 1999.



**MATERIAL EXAMINED:** Material was examined from following countries: Algeria; Armenia; Austria: Niederösterreich, Oberösterreich, Steiermark; Croatia; Czech Republic; France: Ain, Haute-Garonne, Haut-Rhin, Nord, Pyrénées Orientales, Tarn; Germany: Baden-Württemberg, Bayern, Berlin, Brandenburg, Nordrhein-Westfalen, Rheinland-Pfalz (♂ lectotype of *Trioza velutina*, paralectotypes 1 ♂, 2 ♀, Boppard), Sachsen, Thüringen (including ♀ holotype of *Trioza distincta*); Greece; Hungary; Italy: Alto Adige, Veneto; Kazakhstan; Mongolia; Russia: European part, Altay, Dagestan, Irkutsk District; Slovakia; Spain: Andalusia, Canaries; Switzerland: Aargau, Bern, Basel-Land, Basel-Stadt, Graubünden, Jura, Schaffhausen, Schwyz, Vaud; Turkey: Kars; Turkmenistan; Ukraine; United Kingdom: England, Scotland (BMNH, MHNG, MMBC, MNHN, NHMB, NHMV, SMTD, ZISP, ZMHB). The following material from the Flor collection (EAUT) was examined: 1 ♂, no 1090 on yellow label, 1 ♀, no 8670 on red label. Both specimens were identified by Flor as *Trioza velutina*. There is no list referring to these particular numbers (O. Kurina, pers. comm.). Their provenience is therefore unknown.

**DIAGNOSIS:** Adult. Total body length 2.0–2.8 mm. Colour of thorax usually dark brown or almost black with exception of area around wing insertion which is yellowish. Younger specimens with light colour more expanded and dark areas greyish rather than black. Genal processes 0.5–0.9 times as long as vertex along mid-line, subacute apically. Forewing (Fig. 4) relatively short and broad, angular apically; bifurcation of vein M near or slightly distal to line connecting apices of veins Rs and Cu<sub>1a</sub>. Surface spinules present in all cells of forewing, forming more or less expanded fields. Hindwing three quarters of forewing length. Male proctiger (Fig. 16) relatively slender, weakly produced posteriorly. Paramere (Fig. 17) slender, lamellar, evenly tapering to apex, blunt apically. Distal portion of aedeagus (Fig. 18) with relatively short apical hook. Female proctiger (Fig. 26) with relatively short, massive apical process, pointed apically; subgenital plate, in profile, bearing small point apically. Measurements as in Table 1.

Fifth instar larva unknown.

**DISTRIBUTION:** Probably widely distributed in the Palaearctic region. There are no reliable literature records as the species has been previously confused with *T. galii*.

**BIOLOGY:** Unknown, probably also on *Galium* spp. on which adults have been collected.

**COMMENTS:** For the validity of the name f. *spinogalii* Šulc see comments on *T. galii*.

***Trioza velutina* Foerster var. *thoracica* Flor, nomen dubium**

*Trioza velutina* Foerster var. *thoracica* Flor, 1861a: 514. Holotype ♀, France: Bouche du Rhône, Gémenos near Marseille (G. Flor), not examined, probably lost (Šulc, 1913: 44).

**COMMENTS:** Flor (1861a) described *Trioza velutina* var. *thoracica* for a single ♀ from Southern France. According to paragraph 45.6.4 of the ICZN (1999) the name *thoracica* has to be regarded as subspecific and as such becomes available. Flor's description is not diagnostic. Furthermore the holotype could not be traced in the collections of the EAUT (O. Kurina, pers. comm.) and NHMV (H. Zettel, pers. comm.) and appears to be lost (Šulc, 1913: 44). For this reason we regard *thoracica* as nomen dubium.

## ACKNOWLEDGEMENTS

For the loan or gift material we are grateful to Javier Blaso-Zumeta (Pina de Ebro), Christian Cocquempot (Montpellier), William Della Guistina (Versailles), Jürgen Deckert (ZMHB), Sakis Drosopoulos (Athens), Rainer Emmrich (SMTD), David Hollis (BMNH), Izya Kerzhner (ZISP), Tanja Kothe (ZSSM), Olavi Kurina (EAUT), David Ouvrard (MNHN), Paolo A. Pedata (DEZA), H. Zettel (NHMV). We thank Ian D. Hodkinson (Liverpool) for his comments on the manuscripts.

## REFERENCES

- AULMANN, G. 1913. Psyllidarum Catalogus. *W. Junk, Berlin*, 92 pp.
- BAEVA, V.G. 1972. New species of psyllids (Homoptera, Psylloidea) from Turkmenia. *Doklady Akademii nauk Tadzhikistoi SSR* 15: 61-63. (In Russian).
- BOSELLI, F.B. 1930. Studi sugli psyllidi (Homoptera: Psyllidae o Chermidae) IV. Biologia e sviluppo della *Spanioza galii aspinovelutina* (Sulc). *Bollettino del Laboratorio di Zoologia generale e agraria del R. Istituto Superiore agrario di Portici* 23: 13-27.
- BURCKHARDT, D. & COUTURIER, G. 1994. The plant-louse *Leuronota calycophylli* sp. n. (Homoptera, Psylloidea), a pest on the timber species *Calycophyllum spruceanum* (Rubiaceae) in Peru. *Bulletin of Entomological Research* 84: 307-312.
- CONCI, C. 1992. *Spanioza tamaninii* sp. n., from Trentino (NE Italy) (Homoptera Psylloidea). *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* 132 (1991): 257-264.
- DOCTERS VAN LEEUWEN, W.M. 1937. New and noteworthy zooecidia from the Netherlands. *Marcellia* 29: 73-86.
- EDWARDS, J. 1896. The Hemiptera-Homoptera (Cicadina and Psyllina) of the British Isles. *L. Reeve and Co., London*, 271 pp.
- ENDERLEIN, G. 1926. Psyllidologica VIII. *Entomologische Mitteilungen* 15: 397-401.
- FLOR, G. 1861a. Die Rhynchoten Livlands, II. Abtheilung Sternorrhyncha Am. et S., 2. Zunft Phytophithres Burm. *Dorpat*, pp. 436-546.
- FLOR, G. 1861b. Zur Kenntniss der Rhynchoten. *Bulletin de la Société Impériale des Naturalistes de Moscou* 34: 331-422.
- FOERSTER, A. 1848. Uebersicht der Gattungen und Arten in der Familie der Psylloden. *Verhandlungen des naturhistorischen Vereins der preussischen Rheinlande* 3: 65-98.
- GEGECHKORI, A.M. & LOGINOVA, M.M. 1990. The psyllids (Homoptera, Psylloidea) of the USSR (an annotated check list). *Akademiya Nauk Gruzinskoy SSR, Tbilisi*, 162 pp. (In Russian).
- HARDY, J. 1853. On some excrescences, etc., on plants occasioned by mites. *Proceedings of the Berwickshire Naturalists' Club* 3 (3): 111-113. Reprinted in *Zoologist* 11: 3875-3877.
- HOUARD, C. 1909. Les zoocécidies des plantes d'Europe et du Bassin de la Méditerranée, volume 2. *Librairie scientifique A. Hermann et Fils, Paris*, pp. 573-1247.
- ICZN International Commission on Zoological Nomenclature 1999. International Code of Zoological Nomenclature, 4th edition. *International Trust for Zoological Nomenclature, London*, 306 pp.
- KIEFFER, J.J. 1889. Mittheilungen über Psylliden. *Entomologische Nachrichten* 14: 222-224.
- KLIMASZEWSKI, S.M. 1973. The jumping plant lice or psyllids (Homoptera Psylloidea) of the Palaearctic: an annotated check list. *Annales zoologici, Warszawa* 30: 155-286.
- LAUTERER, P. 1982. New data on the occurrence, bionomics and taxonomy of some Czechoslovakian Psylloidea (Homoptera). *Acta Musei Moraviae, Scientiae naturales* 67: 133-162.
- LETHERRY, L. 1874. Catalogue des Hémiptères du Département du Nord, 2nd edition. *Imprimerie L. Danel, Lille*, 108 pp., 2 plates.

- LOGINOVA, M.M. 1978. New species of psyllid (Homoptera, Psylloidea). *Trudy Zoologicheskogo Instituta* 61: 30-123. (In Russian).
- LÖW, F. 1882. Revision der paläarktischen Psylloden in Hinsicht auf Systematik und Synonymie. *Verhandlungen der zoologisch-botanischen Gesellschaft Wien* 32: 227-254.
- OSHANIN, B. 1907. Verzeichnis der palaearktischen Hemipteren mit besonderer Berücksichtigung ihrer Verteilung im Russischen Reiche, volume 2 Homoptera, part 2. *Druckerei der Kaiserlichen Akademie der Wissenschaften, St. Petersburg*, pp. 193-384.
- OSSIANNILSSON, F. 1992. The Psylloidea (Homoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica* 26, 346 pp.
- SCOTT, J. 1876. Monograph of the British species belonging to the Hemiptera-Homoptera, family Psyllidae; together with the description of a genus which may be expected to occur in Britain. *Transactions of the entomological Society* 4: 525-569, plates 8-9.
- ŠULC, K. 1910. Monographia generis *Trioza* Foerster, pars I. *Sitzungsberichte der königlich-böhmischen Gesellschaft für Wissenschaften II Klasse* 1-34, plates 1-10.
- ŠULC, K. 1913. Monographia generis *Trioza* Foerster, pars IV. *Sitzungsberichte der königlich-böhmischen Gesellschaft für Wissenschaften II Klasse* 1-48, plates 34-48.
- TUTHILL, L.D. 1943. The psyllids of America north of Mexico (Psyllidae: Homoptera). *Iowa State College Journal of Science* 17: 443-660.
- WAGNER, W. & FRANZ, H. 1961. Überfamilie Sternorrhyncha (Psylloidea). In: FRANZ, H. (ed.). *Die Nordostalpen im Spiegel ihrer Landtierwelt*, vol. 2. *Innsbruck*, pp. 158-179.
- WHITE, I.M. & HODKINSON, I.D. 1982. Psylloidea (Nymphal Stages) Hemiptera, Homoptera. *Handbooks for the Identification of British Insects* 2(5b), 50 pp.



## **A new species of *Diathrausta* Lederer, 1863 from Africa (Lepidoptera, Pyraloidea, Crambidae, Spilomelinae)**

Koen MAES

Present address: Royal Museum for Central Africa, Leuvensesteenweg 13,  
B-1380 Tervuren, Belgium.

Address: AgroBioSys Intl., Kl.Smetledestraat 192, B-9230 Wetteren, Belgium.

Email: kvmaes@belgacom.net

**A new species of *Diathrausta* Lederer, 1863 from Africa (Lepidoptera, Pyraloidea, Crambidae, Spilomelinae).** - *Diathrausta semilunalis* sp. n. is described from Southern Africa. The adult, genitalia, and tympanal organs are illustrated. Its placement in *Diathrausta* is discussed. *Cangetta fulviceps* (Hampson, 1917) comb. n. is excluded from the genus *Diathrausta*.

**Keywords:** *Diathrausta semilunalis* sp. n., Africa

### INTRODUCTION

Lederer (1863) erected the genus *Diathrausta* for his new species *Diathrausta profundalis* from "Amboina" [Indonesia].

Nine species were later added by Hampson (1903, 1917), Dyar (1913) and Druce (1899) mostly from the Old and New World tropics.

Munroe (1956) reviewed the North American species of *Diathrausta*, recognizing two species and three subspecies. He is the first to illustrate the male genitalia of some species in this genus. In total there are now 18 species in this genus (personal database).

Only one species, *Diathrausta fulviceps* Hampson, 1917 (Malawi), has been described from Africa. Presumably, it was placed in *Diathrausta* based on external similarities. I dissected specimens of *D. fulviceps* from Kenya, Tanzania and the Democratic Republic of Congo and compared the genitalia with those of *Diathrausta reconditalis* (Walker, 1859) and *D. harlequinialis amaura* Munroe, 1956 as illustrated in Munroe (l.c.). The male genitalia of *D. fulviceps* have a simple uncus broadly fused with the tegumen and dorsally with some simple setae, this is in sharp contrast with the narrow slender uncus of true *Diathrausta* species. The valva of *D. fulviceps* are broad at their base with the tegumen and narrowing near the apex, not ear-shaped as in true *Diathrausta* species. *D. fulviceps* has also a large fibula in the median part of the valva. The saccus is very large in *D. fulviceps* and almost absent in the true *Diathrausta* species. *D. fulviceps* does not belong in *Diathrausta* and is tentatively placed in the genus *Cangetta* because of the resemblance in structure of the fibula in the male genitalia. It differs with true *Cangetta* species in the structure of the uncus, which is simple

in *Cangetta fulviceps* comb. n., but strongly modified, bilobed and carrying long setae in most true *Cangetta* species.

During the curation of collections in various museums a striking undescribed species from southern Africa came to my attention. The male genitalia have the same basic structure (simple slender uncus, ear-shaped valva, fibula near base of valva) as found in *Diathrausta* species as illustrated by Munroe (1956). This new species is therefore placed in the genus *Diathrausta*. Pictures of the male and female genitalia are given, this is the first time the female genitalia of this genus is illustrated.

Abbreviations used:

ABSRC AgroBioSys Reference Collection, Wetteren, Belgium.

MHNG Muséum d'histoire naturelle, Genève, Switzerland.

RMCA Royal Museum for Central Africa, Tervuren, Belgium.

TMP Transvaal Museum, Pretoria, South Africa.

*Diathrausta semilunalis* sp. n.

Pl. 1, 2 A-D

TYPE MATERIAL: Holotype ♂: [SOUTH AFRICA] Karkloof, Natal, 15.Jan.[19]17 A.J.T.Janse, K.Maes Gen.prep.nr.♂20719 (TMP); 10 Paratypes: 1♀: [SOUTH AFRICA] Marieps Mnt., Dec.1925, G.van Son, K.Maes Gen.prep.nr.♀20738 (TMP); 1♀: [SOUTH AFRICA] Mahuba's Kl., 1050m, 14.i.[19]25, A.J.T.Janse (abdomen lost) (TMP); 1♂: [SOUTH AFRICA] Mahuba's Kl., 1050m, 16.i.[19]25, A.J.T.Janse (ABSRC); 1♀: [SOUTH AFRICA] Barberton, 25.i.1911, A.J.T.Janse (TMP); 1♀: [SOUTH AFRICA] Karkloof, Natal, 21.i.[19]17 (ABSRC); 1♀: [SOUTH AFRICA] Rietvlei, 1.4.[19]18, Coll.Janse (TMP); 1♂: [SOUTH AFRICA] Sabie, Tvl., 30.iv.-5.v.1977, J.H.Potgieter, c.s. (TMP); 1♂: [DEMOCRATIC REPUBLIC OF CONGO] Elisabethville, iv-v.1952, Ch.Seydel (RMCA); 1♀: [DEMOCRATIC REPUBLIC OF CONGO] Elisabethville, xii.1936, Ch.Seydel, K.Maes Gen.prep.nr.♀14305 (RMCA); 1♂: [DEMOCRATIC REPUBLIC OF CONGO] Ht.Katanga, Midingi, 1.vii.[19]30, J.Romieux (MHNG).

DISTRIBUTION: South Africa, Democratic Republic of the Congo.

ETYMOLOGY: The name refers to the half-moon shaped white spot between the upper angle of the cell in the fore wing and the costa.

DIAGNOSIS: Fore wings triangular with a half-moon shaped white or cream-white spot between the upper angle of the cell and the costa.

DESCRIPTION:

*Head*: frons rounded; labial palps porrect, length about twice diameter of compound eye, basal part of first segment white or creamy-white, otherwise brown; maxillary palps long, brown.

*Thorax and abdomen*: dark brown like ground colour of fore wings; legs brown, spurs 0,2,4; abdomen dark brown.

*Wings*: fore wings triangular; ante- and post-medial lines black, almost continuous for entire length, orbicular and reniform stigma dark; costa black near wing base; half-moon shaped white or creamy-white spot near upper angle of cell, on outer side delimited by black postmedial line; apex brown as rest of wing, fringe on fore and hind wings with black and white or creamy-white parts; hind wings lighter brown or black as fore wings with narrow white or creamy-white postmedial line; wing pattern



PLATE 1

Adult moth: *Diathrausta semilunalis* sp.n. Holotype (black bar = 1 cm)

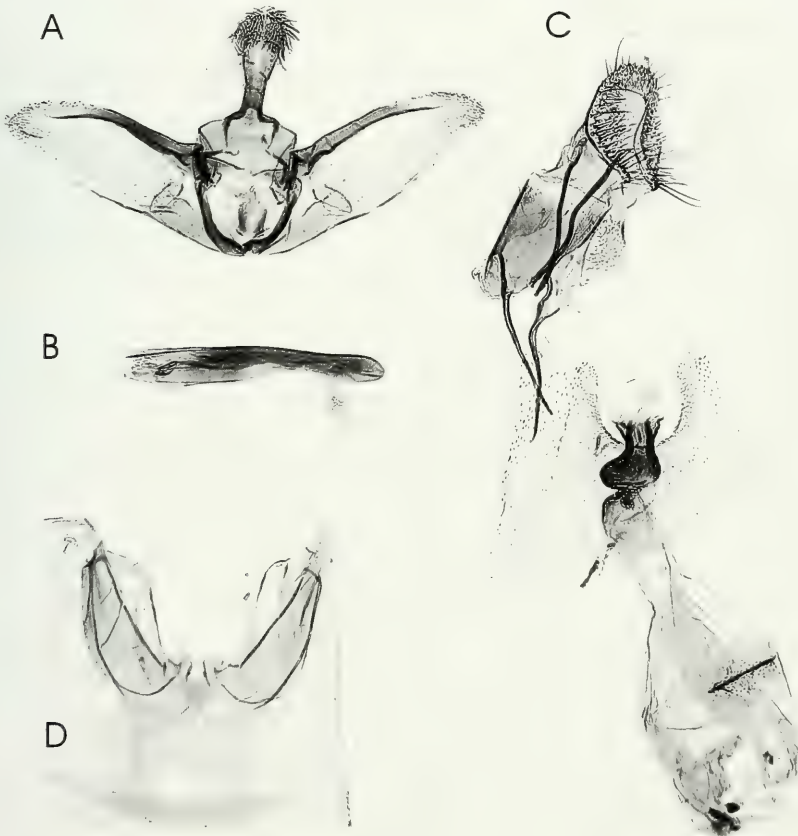


PLATE 2

Genitalia and tympanal organs *Diathrausta semilunalis* sp.n. A: male genitalia. B: aedeagus of male genitalia. C: female genitalia. D: tympanal organs.



more or less evident or largely reduced in dark specimens; frenulum simple in males, double in females; retinaculum a series of elongated scales near Cu-stem of fore wing; wingspan: 13-16mm.

*Tympanal organs* (Pl. 2 D): partly invaginated with broad fornix tympani.

*Male genitalia* (Pl. 2 A B): uncus a single large lobe, dorsally covered with short setae; tegumen almost rectangular, vinculum U-shaped, saccus very small; valva with strong costa, more membranous near apex and with a few short setae; spatula-shaped fibula medially at base of valva; juxta shield-shaped; tubular aedeagus with a single spine-shaped cornutus.

*Female genitalia* (Pl. 2 C): papillae anales with short and long setae; apophyses posteriores and anteriores of about same length; sinus vaginalis invaginated at VIIIth sternite, forming circular membranous area; calyx-shaped, well-sclerotized ostium bursae; ductus bursae membranous and rather short; corpus bursae bulbous with plate-shaped signum carrying straight transversal ridge; appendix bursae lacking.

LIFE CYCLE: unknown.

## ACKNOWLEDGEMENTS

I wish to thank Dr. M. Kruger and Mrs. B. Dombrowsky from the Transvaal Museum in Pretoria, Dr. Bernard Landry from the Muséum d'histoire naturelle in Geneva, and Dr. Marc De Meyer and Dr. Ugo Dall'Asta from the Royal Museum for Central Africa for putting material of their collections at my disposal.

This paper results from research finalized during a project funded by DWTC (Federale Diensten voor Wetenschappelijke, Technische en Culturele Aangelegenheden), Belgium.

## LITERATURE

- DRUCE, H. 1899. Biologia Centrali-Americana Insecta. *Lepidoptera-Heterocera* vol.ii :537-569.
- Dyar, H. G. 1913. A note on *Diathrausta nerinalis* Walker (Lepidoptera, Pyralidae). *Insecutor Inscitiae Menstruus* 1: 100-102.
- HAMPSON, G. F. 1903. The moths of India. Supplementary Papers to the Volumes in "The Fauna of British India." Series ii. Part x. *Journal of the Bombay Natural History Society* xv(2): 206-226, 1 pl.
- HAMPSON, G. F. 1917. Descriptions of New Pyralidae of the Subfamilies Hydrocampinae, Scoparinae &. *The Annals and Magazine of Natural History* (8)20: 201-216.
- LEDERER, J. 1863. Beitrag zur Kenntniss der Pyralidinen. *Wiener Entomologische Monatschrift* 7(8): 243-280; (10): 331-378; (11): 379-506, 18pl.
- MUNROE, E. 1956. The North American species of *Diathrausta* Lederer (Lepidoptera: Pyralidae). *The Canadian Entomologist* 88: 579-583, 7 figs.

## Redescription of *Ceratophysella lawrencei* (Gisin, 1963) (Collembola: Hypogastruridae)

Dariusz SKARŻYŃSKI

Zoological Institute, Wrocław University, Przybyszewskiego 63/77, 51-148 Wrocław, Poland. E-mail: hypogast@biol.uni.wroc.pl

**Redescription of *Ceratophysella lawrencei* (Gisin, 1963) (Collembola: Hypogastruridae).** - *Ceratophysella lawrencei* (Gisin, 1963) is redescribed based on material from Switzerland (types), Austria, Italy and Poland. A lectotype is designated. Notes on morphology of the closely related species *Ceratophysella neomeridionalis* (Nosek & Červek, 1970) are given.

**Keywords:** Collembola - Hypogastruridae - *Ceratophysella lawrencei* - *Ceratophysella neomeridionalis* - taxonomy - Europe.

### INTRODUCTION

During a faunistic survey in the Tatra National Park (S Poland) numerous *Ceratophysella* specimens with 2 + 2 spine-like setae on the head were found. Identification led to *C. lawrencei* with some doubts. This species is insufficiently known and available literature does not allow to recognize it unambiguously (Thibaud *et al.*, 2004). Therefore, a redescription is presented here.

Gisin (1949) briefly described *Hypogastrura gibbosa* (Bagnall, 1940) with 2 + 2 spine-like setae on the head from the Swiss Alps. Later in "Collembolenfauna Europas" (Gisin, 1960) he repeated the short species diagnosis and noticed that the identity of British and Swiss specimens of *H. gibbosa* is doubtful. His suspicion turned out to be true when Lawrence (1962) redescribed this species based on Bagnall's types from Great Britain. He stated that *H. gibbosa* sensu Gisin 1949, 1960 with cephalic spines refers to a different species. As a consequence Gisin (1963) established a new species, *H. lawrencei* by giving a reference to previous descriptions (Gisin, 1949, 1960).

Examination of Gisin's material allowed to redescribe this species using a set of modern diagnostic characters (Fjellberg, 1984, 1998/1999; Babenko *et al.*, 1994; Skarżyński, 2004). Moreover, a lectotype was designated.

### *Ceratophysella lawrencei* (Gisin, 1963)

*Hypogastrura lawrencei* Gisin, 1963: 97.

*Hypogastrura gibbosa* (Bagnall, 1940): Gisin 1949, 1960 nec Bagnall, 1940.

TYPE MATERIAL: Lectotype - male on slide (formerly in alcohol), by present designation; He 242a: Grisons, Swiss National Park, Plan Possa (above Il Fuorn), S slope, *Pineto-Caricetum humilis*, 1900 m a. s. l., 13. V. 1945, soil sample (1-4 cm) (in the collection of the Muséum d'histoire naturelle in Geneva), paralectotypes - 5 specimens of unidentified sex on slides (one of them formerly in alcohol), same data as lectotype.

OTHER MATERIAL EXAMINED: 3 specimens of unidentified sex on slide; He 422: Grisons, Swiss National Park, Il Fuorn, S slope, on the way to Plan Posa, *Mugeto-Ericetum caricetosum humilis*, 1850 m a. s. l., on mushrooms, 22-24.VIII. 1950. 2 specimens of unidentified sex on slide; Törne, [illegible inscription - probably one of collecting sites of *H. cf. gibbosa* in Austria mentioned in Törne (1958)], 27.II.1951 (the material is preserved in the collection of the Muséum d'histoire naturelle in Geneva). 1 female, 3 juveniles on slide; moss on calcareous rocks (ca. 2000 m a. s. l.), neighborhood of Cortina d'Ampezzo (Dolomites, Alps, N Italy), 20.VI-II.1993, leg. D. Skarżyński. 12 males, 10 females, 8 juveniles on slides; moss and mountain grasslands with mushrooms on calcareous rocks: deep ravine Kraków (ca. 1100 m a. s. l.), entrance to the cave Mylna (ca. 1100 m a. s. l.), N slope of the Gładkie Uplaziańskie (ca. 1600 m a.s.l.), W slope of the Chuda Turnia (ca. 1800 m a. s. l.) (Tatra Mountains, Carpathians, S Poland), 18.VI.2004, 19.VIII.2004, leg. D. Skarżyński (the material is preserved at the Department of Biodiversity and Evolutionary Taxonomy, Wrocław University, Poland).

DIAGNOSIS: This species can be recognized by the following set of characters: fields of coarse granulation on head, thoracic and abdominal terga present, dorsal chaetotaxy of the *C. armata*-type, setae long, thick and serrated, setae  $d_2$  and  $oc_2$  on head spine-like, setae  $p_3$  on abdominal tergum IV present, antennal segment IV with ca. 25 modified ventral sensilla, eversible sac between antennal segments III-IV present, head of maxilla and labium of the *C. armata*-type, outer lobe with 1 sublobal hair, empodial appendage with long apical filament reaching distinctly beyond inner tooth of claws, dens with uniform, fine granulation and 7 setae (2-4 inner setae modified), mucro boat-like with large lateral lamella, anal spines large, curved, situated on high basal papillae.

REDESCRIPTION: Body length 0.9-1.6 mm (lectotype, male 0.95 mm). Colour of the body dark greyish-violet (in freshly collected specimens from the Tatra Mts, greyish-brown in alcoholic lectotype and paralectotype), legs and ventral part of the body paler, eyes fields black, anal spines yellow.

Integument with fine granules and fields of coarse granulation on head (large uniform field covering almost whole dorsal side excluding bases of antennae), thoracic terga II-III (two subaxial fields of medium size), abdominal terga I-III (small fields around macrochaetae  $p_2$ ), abdominal tergum IV (one axial field of medium size and two lateral large ones), abdominal terga V-VI (large fields covering almost whole surface) (Figs 1-3). Fields made of rather irregularly distributed granules, which are broad, moderately high and sometimes bent in different directions (Figs 1-3). On abdominal tergum V coarse granules are usually loosely distributed from the line extended between setae  $a_1$  to the line extended between setae  $p_1$ , behind this line granules are slightly smaller and densely packed. 8-10 granules between setae  $p_1$  (Fig. 3).

Dorsal chaetotaxy as in Figs 1-3. Microchaetae and macrochaetae (especially on last abdominal terga) long, thick and serrated (Figs 1-3). Body sensilla (s) short, thin and smooth. Setae  $d_2$  and  $oc_2$  on head spine-like in unreprouductive adults (Fig. 1), in juveniles like normal or thickened macrochaetae, rarely spine-like. Setae  $a_2$  on thoracic tergum II like mesochaetae or macrochaetae. Setae  $p_1$  and  $p_2$  on abdominal tergum IV macrochaetae and microchaetae respectively, setae  $p_3$  present. Subcoxae I, II, III with 1, 2, 3 setae respectively. Microsensillum (ms) on thoracic tergum II present.

Antennal segment IV with simple apical vesicle, subapical organite, micro-sensillum, 7 cylindrical sensilla in typical arrangement and ca. 25 short, thick, curved



and flattened at tips sensilla in ventral file (Fig. 5). Antennal III-organ with two long (lateral) and two short (internal) curved sensilla. Microsensillum on antennal segment III present. Eversible sac between antennal segments III-IV present (Fig. 5). Antennal segment I with 7 setae.

Ocelli 8+8, G and H slightly smaller than others (Fig. 1). Postantennal organ about twice as large as single ocellus, with 4 lobes of which the anterior pair is distinctly larger than the posterior (Fig. 4). Large accessory boss partly surrounded by posterior lobes of postantennal organ (Fig. 4).

Labrum with 5, 5, 4 setae and 4 prelabrals. Head of maxilla of the *C. armata*-type (see Fjellberg, 1984). Outer lobe with 1 sublobal hair. Labium of the *C. armata*-type (see Fjellberg, 1998/1999).

Tibiotarsi I, II, III with 19, 19, 18 setae respectively, clavate setae absent. Claws with inner tooth and pair of lateral teeth (Fig. 6). Empodial appendage with broad basal lamella and long apical filament reaching beyond inner tooth of claws (Fig. 6), ratio: empodial filament/ inner edge of claws = 0.7-1 (0.5-0.7 in the Tatra Mts population).

Ventral tube with 4+4 setae.

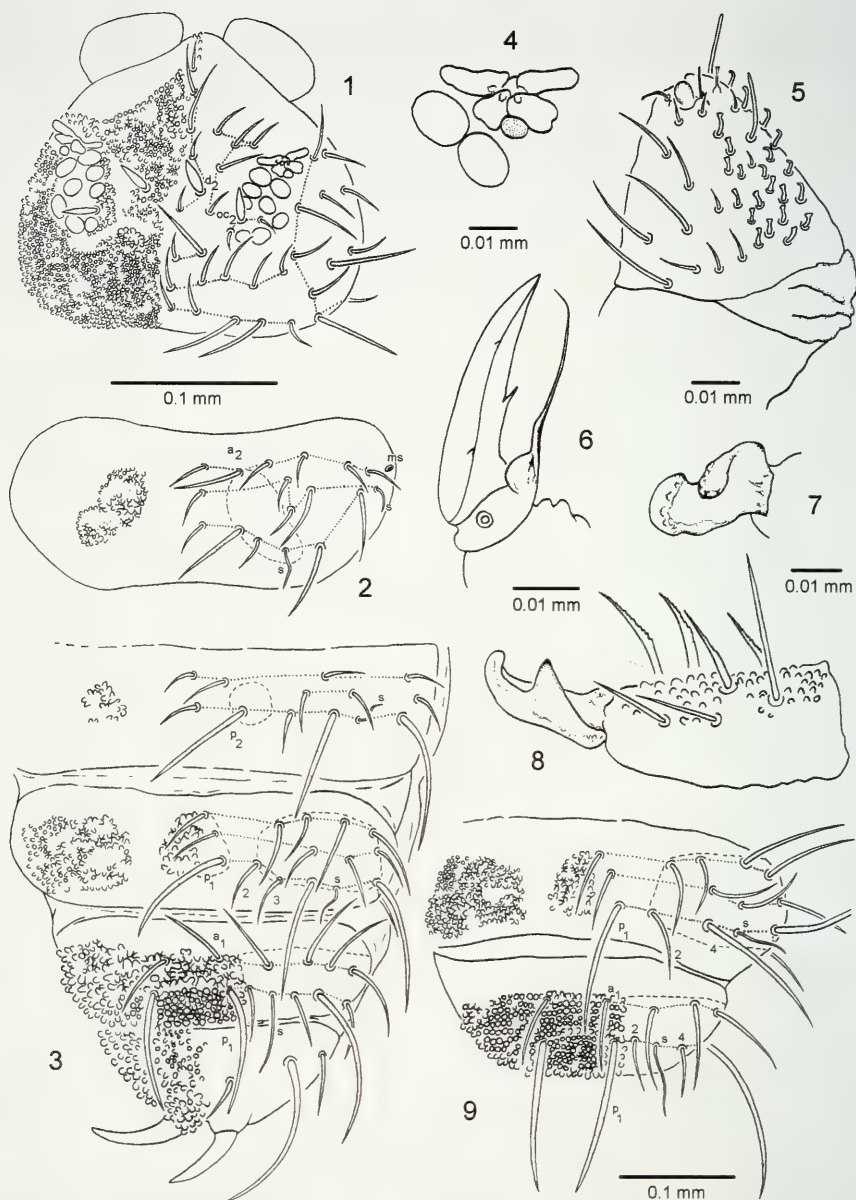
Furca fully developed. Dens with uniform, fine granulation and 7 setae (2-4 inner setae modified) (Fig. 8). Mucro boat-like, with large lateral lamella (Figs 7, 8). Ratio: dens/mucro = ca. 2. Retinaculum with 4+4 teeth.

Anal spines large, curved, situated on high basal papillae (Fig. 3). Ratio: anal spines/inner edge of claws III = ca. 1.5.

DISCUSSION: *C. lawrencei* resembles these species of the *C. armata*-group which have integument with fields of coarse granulation. It distinctly differs from *C. granulata* Stach, 1949 and *C. scotica* (Carpenter & Evans, 1899) in having spine-like setae on head (v. absent) and from *C. silvatica* (Rusek, 1964) in their number (*C. lawrencei*: 2 + 2, v. 1 + 1). This species is also easy to distinguish from *C. franzi* (Butschek & Gisin, 1949) by different arrangement of cephalic spine-like setae (*C. lawrencei*:  $d_2$  and  $oc_2$ , v.  $d_2$  and  $sd_5$ ).

Undoubtedly *C. lawrencei* is closely related to *C. neomeridionalis* (Nosek & Červek, 1970) – a species described from the Slovenian Dinaric Mountains (Nosek & Červek, 1967, 1970) and also known from the Polish Carpathians (Weiner, 1981, Smolis *et al.*, 2001, Skarżyński & Smolis, 2002, Smolis & Skarżyński, 2003). They differ in the structure of empodial appendage (*C. lawrencei*: basal lamella broad, apical filament long reaching beyond inner tooth of claws, v. basal lamella small, apical filament short reaching distinctly below inner tooth of claws) and arrangement of setae on abdominal tergum IV (*C. lawrencei*: setae  $p_3$  present, v. setae  $p_3$  absent).

Nosek & Červek (1967) considered chaetotaxy of the last abdominal terga of *C. neomeridionalis* characteristic for this species. However this opinion seems to be a result of erroneous identification of some setae. It is evident after examination of paratype from the collection of the Muséum d'histoire naturelle in Geneva (Nanos, 7.XI.64, leg. S. Červek) and specimens collected in the Polish Carpathians that they have body sensilla on abdominal tergum IV in typical position  $p_5$  (Fig. 9) ( $p_7$  in original description, see Nosek & Červek, 1967: 247, Fig. 8), setae  $p_1$  on abdominal tergum V as strong macrochaetae, setae  $p_2$  and  $p_4$  as short microchaetae and long body



FIGS 1-9

*Ceratophysella lawrencei* (1-8): 1, chaetotaxy and granulation of head; 2, chaetotaxy and distribution of coarse granulation fields on thoracic tergum II; 3, chaetotaxy and distribution of coarse granulation fields on abdominal terga III-VI; 4, postantennal organ, accessory boss and neighbour ocelli; 5, ventral side of antennal segments III-IV; 6, claw of legs I; 7, mucro; 8, dens and mucro, lateral view. (1-4, 6: lectotype; 5, 7, 8: specimen from Tatra Mts). *Ceratophysella neomeridionalis*: 9, chaetotaxy and distribution of coarse granulation fields on abdominal terga IV-V (paratype). Abbreviations in text.

sensilla (Fig. 9) (in original description  $p_1$  is short microchaeta,  $p_2$  is long microchaeta, sensillum is short and  $p_4$  is macrochaeta, see Nosek & Červek, 1967: 247, Fig. 8).

**DISTRIBUTION:** *C. lawrencei* was recorded from the Swiss, Austrian and Italian Alps, the Appenines (Gisin, 1949, 1960, 1963; Törne, 1958; Christian, 1987; Dallai *et al.*, 1995) and for the first time from the Polish Tatra Mts (Carpathians).

**ECOLOGICAL REMARKS:** *C. lawrencei* seems to prefer different microhabitats (soil, forest litter, moss tufts, mountain grasslands, mushrooms) associated with calcareous rocks in the mountains at an altitude 900-2000 m a. s. l.

## ACKNOWLEDGEMENTS

I wish to express my sincere thanks to Dr Charles Lienhard from the Muséum d'histoire naturelle in Geneva for supplying Gisin's material of *C. lawrencei* and a paratype of *C. neomeridionalis*. I am also grateful to the management of the Tatra National Park for their help with my investigations. The study was sponsored by the Wrocław University (grant 2020/W/IZ/2004).

## REFERENCES

- BABENKO, A. B., CHERNOVA, N. M., POTAPOV, M. B., STEBAEVA, S. K. 1994. Collembola of Russia and adjacent countries: Family Hypogastruridae. *Nauka, Moscow*, 336 pp.
- CHRISTIAN, E. 1987. Catalogus Faunae Austriae. XIIa, U. Kl.: Collembola (Springschwänze). *Verlag der Österreichischen Akademie der Wissenschaften, Wien*, 80 pp.
- DALLAI, R., MALATESTA, E., RAMELLINI, P. 1995. Apterygota: Collembola, Protura, Microcoryphia e Zygentoma (=Thysanura s.l.), Diplura. In: MINELLI, A., RUFFO, S., LA POSTA, S. (eds). Checklist delle specie della fauna italiana, 33. *Calderini, Bologna*, 25 pp.
- FJELLBERG, A. 1984. Maxillary structures in Hypogastruridae (Collembola). *Annales de la Société Royale Zoologique de Belgique* 114: 89-99.
- FJELLBERG, A. 1998/1999. The Labial Palp in Collembola. *Zoologischer Anzeiger* 237: 309-330.
- GISIN, H. 1949. Notes sur les Collemboles avec description de quatorze espèces et d'un genre nouveaux. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 22: 385-400.
- GISIN, H. 1960. Collembolenfauna Europas. *Muséum d'histoire naturelle, Genève*, 312 pp.
- GISIN, H. 1963. Collemboles d'Europe V. *Revue suisse de Zoologie* 70: 77-101.
- LAWRENCE, P. N. 1962. A review of Bagnall's *Hypogastrura* types (Collembola). *Entomologist's Gazette* 13: 132-151.
- NOSEK, J. & ČERVEK, S. 1967. A new species of springtail from the mediterranean region *Hypogastrura (Ceratophysella) meridionalis* sp. n. (Collembola: Hypogastruridae). *Acta Societatis Zoologicae Bohemoslovenicae* 31: 245-249.
- NOSEK, J. & ČERVEK, S. 1970. Beseitigung eines Homonyms in der Gattung *Hypogastrura* (Insecta: Collembola). *Revue suisse de Zoologie* 77: 207.
- SKARŻYŃSKI, D. 2004. Taxonomic position of *Ceratophysella granulata* STACH, 1949 and *Ceratophysella silvatica* (RUSEK, 1964) in the light of morphological and laboratory hybridisation studies. *Acta Zoologica Cracoviensia* 47: 147-153.
- SKARŻYŃSKI, D. & SMOLIS, A. 2002. Notes on *Willemia virae* Kaprus' and *Anurida carpatica* Babenko, two springtails new for the Polish fauna, with remarks on other Collembola collected in caves of the Beskid Niski Mountains (Polish Carpathians). *Polskie Pismo Entomologiczne* 71: 301-306.
- SMOLIS, A., SKARŻYŃSKI, D. & POMORSKI, R. J. 2001. Nowe i rzadkie w faunie Polski gatunki skoczogonków (Collembola). *Przegląd Zoologiczny* 45: 227-230 [in Polish].



- SMOLIS, A. & SKARŻYŃSKI, D. 2003. Springtails (Collembola) of the "Przełom Jasiołki" reserve in the Beskid Niski Mountains (Polish Carpathians). *Fragmenta Faunistica* 46: 121-129.
- THIBAUD, J.-M., SCHULZ, H.-J. & GAMA, M. M. da. 2004. Synopses on Palearctic Collembola. Hypogastruridae. Vol. 4, *Abhandlungen und Berichte des Naturkundemuseums Görlitz* 75(2): 1-287.
- TÖRNE, E. von 1958. Faunistische Befunde einer Untersuchung des Collembolenbesatzes im Excursionsgebiet von Innsbruck. *Acta Zoologica Cracoviensia* 2: 637-680.
- WEINER, W. M. 1981. Collembola of the Pieniny National Park in Poland. *Acta Zoologica Cracoviensia* 25: 417-500.

**Description of *Ceratophysella robustiseta* sp. n. from greenhouses in England, with notes on synonymy of *C. postantennalis* Yosii, 1966 and taxonomic status of *C. morula* Deharveng & Bourgeois, 1991 (Collembola: Hypogastruridae)**

Dariusz SKARŻYŃSKI<sup>1</sup> & Adrian SMOLIS<sup>1</sup>

<sup>1</sup> Zoological Institute, Wrocław University, Przybyszewskiego 63/77, 51-148 Wrocław, Poland. E-mail: hypogast@biol.uni.wroc.pl, adek@biol.uni.wroc.pl

**Description of *Ceratophysella robustiseta* sp. n. from greenhouses in England, with notes on synonymy of *C. postantennalis* Yosii, 1966 and taxonomic status of *C. morula* Deharveng & Bourgeois, 1991 (Collembola: Hypogastruridae).** - *Ceratophysella robustiseta* sp. n. from greenhouses in Kew Gardens (London, England) is described. Notes on morphology and taxonomic status of a related species *Ceratophysella morula* Deharveng & Bourgeois, 1991 are given. *Ceratophysella postantennalis* Yosii, 1966 is synonymized with *Hypogastrura nepalica* Yosii, 1966, syn. n.

**Keywords:** Collembola - Hypogastruridae - *Ceratophysella* - taxonomy.

## INTRODUCTION

The large genus *Ceratophysella* Börner, 1932 comprises three species with a moruliform postantennal organ: *C. mosquensis* (Becker, 1905) from Europe, *C. postantennalis* Yosii, 1966 from Nepal, and *C. morula* Deharveng & Bourgeois, 1991 from Thailand. The first species mentioned is well known and widely distributed (Babenko *et al.*, 1994) while the two latter ones are known from the type locality (*C. morula*) or some localities only (*C. postantennalis*). During visit in Kew Gardens greenhouses in London several specimens which generally resemble *C. postantennalis* and *C. morula* were found. A comparison with the type material of these species made it possible to ascertain that the English specimens represented a new species, *C. morula* requires taxonomic comments and *C. postantennalis* is synonymous with *Hypogastrura nepalica* Yosii, 1966.

## RESULTS AND DISCUSSION

### *Hypogastrura nepalica* Yosii, 1966

*Ceratophysella postantennalis* Yosii, 1966 **syn. n.**

**MATERIAL EXAMINED:** Holotype - specimen in alcohol, Maedane Karka, East Nepal, 10.VI. 1963, leg. Yasuda; paratypes - 6 specimens on slides (formerly in alcohol), same data as holotype. All material deposited in the Muséum d'histoire naturelle in Geneva.

Holotype of *Ceratophysella postantennalis* - male on slide (formerly in alcohol), Nepal, Maedane Karka, 10-12.VI.1963, leg. Yasuda, det. Yosii; paratypes - 9 specimens on slides (formerly in alcohol), Nepal, Maedane Karka, 10.VI.1963, m-2, leg. Yasuda, det. Yosii 1983; 2 specimens on slides (formerly in alcohol), Nepal, Maedane Karka, 12.VI.1963, m-6, leg. Yasuda, det. Yosii 1983. All material deposited in the Muséum d'histoire naturelle in Geneva.

#### REMARKS

*C. postantennalis* was described from Maedane Karka (the Rolwaling Himal, East Nepal) on the basis of specimens with distinct morphological features: moruli-form postantennal organ, short setae, small mucro without lamellae and the presence of a median hump on abdominal tergum V (Yosii, 1966). Bourgeois & Cassagnau (1972) stated an opinion that the taxonomic status of *C. postantennalis* should be revised considering the low diagnostic value (possible epistatic and ecomorphic changes) of the discriminant features used by Yosii.

Examination of the types of *C. postantennalis* showed that the holotype and two paratypes were conspecific with *Hypogastrura nepalica* Yosii, 1966. This synonymy was confirmed by examination of the *H. nepalica* holotype and paratypes. It was interesting that all the studied *H. nepalica* specimens had a median hump on abdominal tergum V similar to this of *C. postantennalis* in fig. 2A of Yosii (1966). Such a structure was not mentioned in the original description of *H. nepalica* (see Yosii, 1966). Among other paratypes of *C. postantennalis* one adult in bad condition (i.e. without head), 6 juveniles (probably of the first instar) of an unidentified *Ceratophysella* (*denticulata*-group) species and 2 unidentified juveniles of the family Hypogastruridae were found. Some of the *Ceratophysella* juveniles had indistinctly folded postantennal organ, long setae, boat-like mucro and median hump on abdominal tergum V absent.

All the data mentioned suggest that Yosii made the *C. postantennalis* description on the basis of *H. nepalica* and the unidentified *Ceratophysella* specimens. Since the holotype of *C. postantennalis* is *H. nepalica* and the taxonomic status of this last species is sufficiently clear, *C. postantennalis* is synonymized here with *H. nepalica*.

#### *Ceratophysella morula* Deharveng & Bourgeois, 1991

*Ceratophysella morula* Deharveng & Bourgeois, 1991: 308

MATERIAL EXAMINED: Holotype - juvenile male on slide, Thailand, Chiang Mai province, Doi Chiang Dao, 1500 m a. s. l., humus at entrance of a shaft, 21.XII.1980, sample THA31, leg. Deharveng (collection of the Muséum National d'Histoire Naturelle in Paris).

#### REMARKS

The status of *C. morula* was questioned by Babenko *et al.* (1994). These authors emphasized the low diagnostic value of the characters which distinguish *C. morula* from the related species *C. mosquensis*: the number of finger-like papillae in the postantennal organ, the ratio dens/mucro and the presence/absence of setae  $a'_2$  on the abdominal tergum V. They also suggested that the original description was inaccurate since  $1 + 1$  v setae on the head and 2 sublobal hairs on the maxillary outer lobe are unique features in the *denticulata*-group. Examination of the holotype of *C. morula* confirmed some critical comments of Babenko *et al.* (1994), in fact  $2 + 2$  v setae and only 1 sublobal hair were visible. Moreover, some other differences between fig. 11 of



Deharveng & Bourgeois (1991) and the real chaetotaxy were noted, for instance the presence of setae  $p_3$  on thoracic tergum II and different lengths of numerous body setae and sensilla. Despite all this, *C. morula* seems to be a good species. From among three subtle characters used by Deharveng & Bourgeois (1991) to distinguish *C. morula* from *C. mosquensis*, the presence/absence of setae  $a'_2$  on abdominal tergum V seems to be reliable. This hypothesis is supported by the results of the study on the taxonomic status of *C. denticulata* (Bagnall, 1941) and *C. engadinensis* (Gisin, 1949) (Skarżyński, 2004). In order to establish the diagnostic value of the remaining characters a study on extensive topotypic material of this species is necessary. The type material of *C. morula* - two juvenile males (holotype - 0.85 mm and 4 + 5 setae on the genital plate) is not suitable for this purpose. Taking this note into consideration one can cautiously expect that the shape of ventral sensilla on antennal segment IV could be a useful feature in diagnostics of the mentioned species (see Tab. 1). *C. morula* is also similar to *C. robustiseta* sp. n. from which it differs clearly in numerous characters presented in Tab. 1.

It is possible that the two populations from Mingbo and Yaral (the Khumbu Himal, East Nepal) recognized as *C. postantennalis* by Yosii (1971) refer in reality to *C. morula*. Examination of respective material from the collection of the Muséum d'histoire naturelle in Geneva (3 adult specimens on slide made by Yosii, Nepal, Mingbo, 299, 3.VI.1961, leg. Janetschek; 12 adult specimens on slides formerly in alcohol, Nepal, Mingbo, 4800 m., 299, 28.V.- 3.VI.1961, leg. Janetschek, det. Yosii; 2 adult specimens on slides formerly in alcohol, Nepal, Yaral, 4100 m., 262, IV.-V.1961, leg. Janetschek, det. Yosii) showed that these specimens generally fit the description of *C. morula*. Nevertheless they clearly differ in the length of setae, *C. morula* has shorter ones. In spite of this it would be premature to regard these Nepalic populations as a new species until more information on the morphological variability of *C. morula* is available.

### *Ceratophysella robustiseta* sp. n.

Figs 1-8

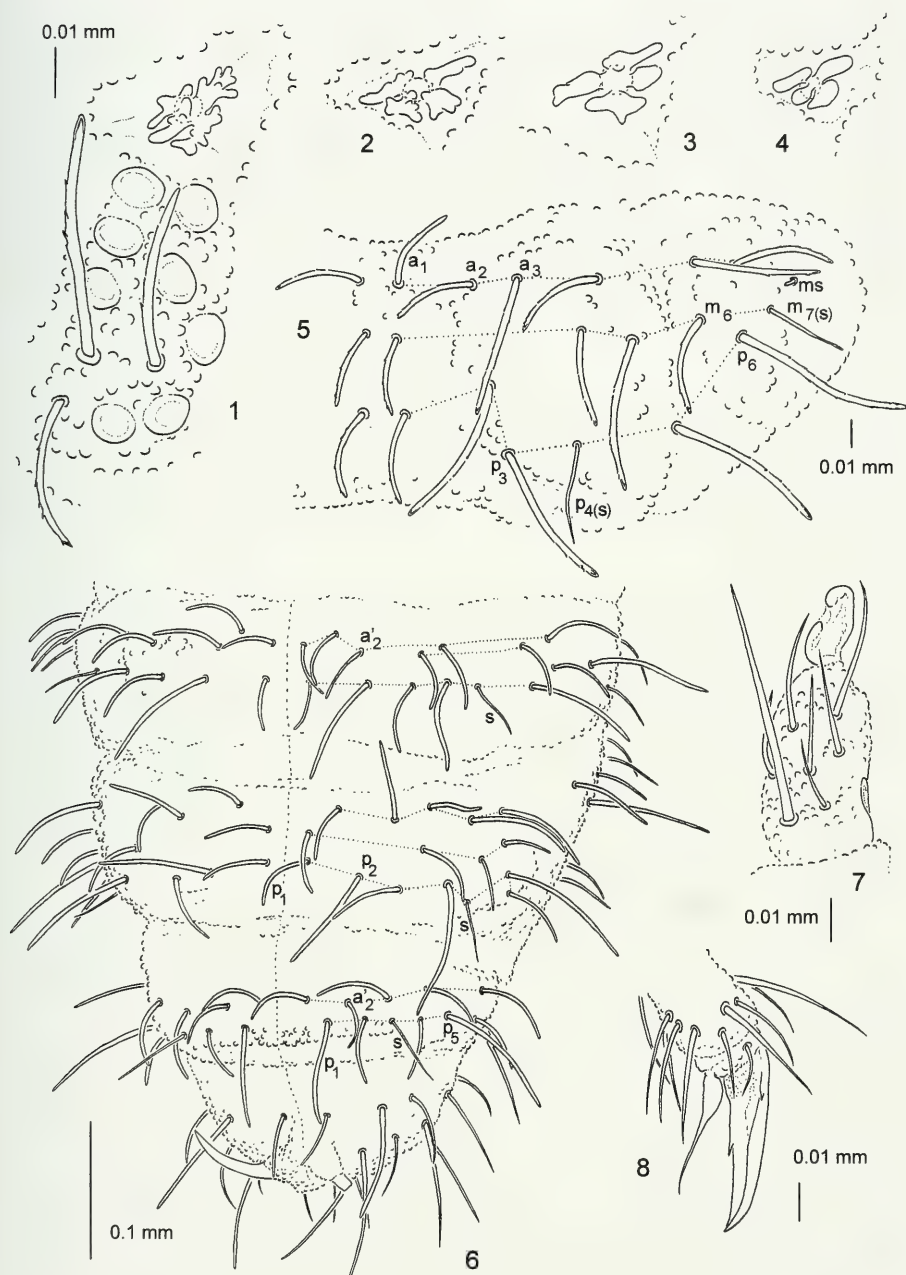
TYPE MATERIAL: Holotype - female on slide, surface of wet mosses near small waterfalls in greenhouses with tropical plants in Kew Gardens (the Evolution House and Princess of Wales Conservatory, London, England), 16. VI. 2003, leg. A. Smolis; paratypes - 12 females, 4 males and 2 juveniles on slides, same data as holotype (type material preserved in the collection of the Department of Biodiversity and Evolutionary Taxonomy, Wrocław University, Poland; one paratype female housed in the collection of the Muséum d'histoire naturelle in Geneva).

ETYMOLOGY: The new species is named after the robust setae on the dorsal side of the body.

DIAGNOSIS: This species is distinguished from other members of the *denticulata*-group by the following combination of characters: eversible sac between antennal segments III-IV absent, antennal segment IV with 10-15 only slightly modified sensilla in ventral file, postantennal organ from almost smooth to weakly moruliform, chaetotaxy with setae  $a'_2$  on abdominal terga I-III and V present, dorsal setae thick abruptly pointed at tips and serrated, empodial appendage with relatively narrow basal lamella

TABLE 1. Morphological differences between species of the *Ceratophysella denticulata*-group having a moruliform postantennal organ.

Characters	<i>C. robustiseta</i> sp.n.	<i>C. morula</i>	<i>C. mosquensis</i>
Ventral sensilla on antennal segment IV	weakly bent and flattened at tips	weakly bent and flattened at tips	distinctly bent and flattened at tips
Eversible sac between antennal segments III-IV	absent	present	present
Postantennal organ	from almost smooth to weakly moruliform	moruliform	moruliform
Dorsal setae	abruptly pointed at tips, serrated, tips with light external layer	gradually tapered, almost smooth, tips without light external layer	gradually tapered, almost smooth, tips without light external layer
Body sensilla	clearly shorter than macrochaetae	little longer than macrochaetae	clearly shorter than macrochaetae
Setae $a'_2$ on abdominal tergum V	present	present	absent
Ratio empodium/claws III	ca 0.75	ca 0.5	ca 0.5
Ratio dens + mucro/inner edge of claws III	ca 1.5	2-2.2	2-2.5
Cuticular skeleton of furca	very delicate	strong	strong
Mucro	small	large	large
Basal macrochaeta on dens	longer than dens	shorter than dens	shorter than dens



FIGS 1-8

*Ceratophysella robustiseta* sp. n.: 1, postantennal organ and ocelli; 2-4, postantennal organ; 5, chaetotaxy of thoracic tergum II; 6, chaetotaxy of abdominal terga III-VI; 7, dens and mucro; 8, tibiotarsus and claw III.



and apical filament reaching about 3/4 of inner edge of claw, furca shortened with very delicate cuticular skeleton, dens with 6-7 unmodified setae, basal macrochaeta longer than dens and mucro small with low lateral lamella.

**DESCRIPTION:** Body length of males 1.1-1.3 mm, females 1.1-1.5 mm. Body colour greyish-black, paler ventrally. Granulation almost uniform, coarser on last abdominal terga, 6-12 granules between setae  $p_1$  on abdominal tergum V. Dorsal chaetotaxy of thorax and abdomen as in Figs 5-6. Chaetotaxy of head typical for the genus. Dorsal macrochaetae and microchaetae relatively short, thick, abruptly pointed at tips and clearly serrated (Figs 1, 5). Tip of dorsal setae usually with light external layer (Fig. 1). Body sensilla short (ratio  $p_3/p_4(s)$  and  $p_6/m_7(s)$  on thoracic tergum II = 1.3-1.5 and 1.6-2 respectively), fine and smooth. Setae  $m_2$  on thoracic terga II-III absent,  $m_6$  present. Setae  $a_3$  on thoracic tergum II distinctly longer than  $a_1$  and  $a_2$ . Microsensillum (ms) on thoracic tergum II present. One additional seta present outside lateral sensillum  $m_7$  on thoracic tergum III (see Deharveng & Bourgeois 1991: 309, Fig. 11). Setae  $a'_2$  on abdominal terga I-III usually present. Setae  $p_1$  on abdominal tergum IV microchaetae,  $p_2$  macrochaetae. Abdominal tergum V with 4 + 4 a-setae inside the two  $p_5$  macrochaetae ( $a'_2$  present). Subcoxae I, II, III with 1, 3(4), 3(4) setae respectively.

Antennal segment IV with simple apical vesicle, subapical organite, microsensillum, 6-7 cylindrical, subequal sensilla in typical arrangement (sensilla d sometimes absent) and about 10-15 thin, slightly curved and blunt-tipped sensilla in ventral file. Antennal III-organ with two long (lateral) and two short (internal) curved sensilla. Microsensillum on antennal segment III present. Eversible sac between antennal segments III-IV absent. Antennal segment I with 7 setae.

Ocelli 8 + 8. Postantennal organ about twice as long as diameter of ocellus B, variable in shape. Four primary lobes of postantennal organ with more or less numerous finger-like papillae (Figs 1-3), sometimes without distinct papillae (Fig. 4). Accessory boss invisible.

Labrum with 5, 5, 4 setae and 4 rounded distal papillae. Four prelabral setae. Head of maxilla as in *C. denticulata* (see Fjellberg, 1984). Maxillary outer lobe with 1 sublobal hair. Labium as in *C. denticulata* (see Fjellberg, 1998/1999), with 6 proximal setae.

Tibiotarsi I, II, III with 19, 19, 18 setae respectively, clavate tenent hairs absent (Fig. 8). Claws with distinct inner tooth and two pairs of indistinct lateral teeth (Fig. 8). Empodial appendage with relatively narrow basal lamella and apical filament reaching about 3/4 of inner edge of claw (Fig. 8). Ventral tube with 4 + 4 setae.

Furca shortened (ratio dens + mucro/inner edge of claws III = ca 1.5), cuticular skeleton of furca very delicate, sometimes invisible. Dens with uniform granulation and 6-7 unmodified dorsal setae (basal macrochaeta longer than dens) (Fig. 7). Mucro small, boat-like with low lamellae (Fig. 7). Retinaculum with 4 + 4 teeth.

Anal spines long (about 1.2 as long as claws III), slightly curved, situated on basal papillae (Fig 6). Colour of anal spines more or less yellowish.

**DISCUSSION:** *C. robustiseta* sp. n. resembles species with a moruliform post-antennal organ such as *C. morula* and *C. mosquensis* from which it differs in the

characters summarized in Tab. 1. Moreover a set of characteristic features: the absence of eversible sac between antennal segments III-IV, the presence of only slightly modified sensilla in ventral file of antennal segment IV, thick dorsal setae, furca shortened with very delicate cuticular skeleton, dens with long basal macrochaeta and small mucro place this species near *C. michalinae* Skarżyński, 2005. Nevertheless it can be easily separated from this species by the following characters (see Skarżyński, 2005): postantennal organ from almost smooth to weakly moruliform (v. smooth), setae  $a'_2$  on abdominal tergum V present (v. absent), empodial appendage with relatively narrow basal lamella and apical filament reaching about 3/4 of inner edge of claw (v. broad basal lamella and apical filament reaching 1/2 of inner edge of claw), 6-7 dental setae (v. 4-7).

#### ACKNOWLEDGEMENTS

We wish to express our sincere thanks to Dr Charles Lienhard for loans of Yosii's material of *C. postantennalis* and *H. nepalica* and to Dr Louis Deharveng for supplying holotype of *C. morula*.

#### REFERENCES

- BABENKO, A. B., CHERNOVA, N. M., POTAPOV, M. B. & STEBAEVA, S. K. 1994. Collembola of Russia and adjacent countries: Family Hypogastruridae. *Nauka, Moscow*, 336 pp.
- BOURGEOIS, A. & CASSAGNAU, P. 1972. La différenciation du type Ceratophysellien chez les Collembolles Hypogastruridae. *Nouvelle Revue d'Entomologie* 2: 271-291.
- DEHARVENG, L. & BOURGEOIS, A. 1991. Two new species of *Ceratophysella* (Collembola: Hypogastruridae) from Thailand. *Acta Zoologica Cracoviensia* 34: 303-310.
- FJELLBERG, A. 1984. Maxillary structures in Hypogastruridae (Collembola). *Annales de la Société Royale Zoologique de Belgique* 114: 89-99.
- FJELLBERG, A. 1999. The Labial Palp in Collembola. *Zoologischer Anzeiger* 237: 309-330.
- SKARŻYŃSKI, D. 2004. Taxonomic status of *Ceratophysella denticulata* (Bagnall, 1941), *C. engadinensis* (Gisin, 1949) and *C. stercoraria* Stach, 1963 (Collembola: Hypogastruridae) in the light of laboratory hybridisation studies. *Insect Systematics and Evolution* 35: 277-284.
- SKARŻYŃSKI, D. 2005. *Ceratophysella michalinae*, a new species from Poland (Collembola: Hypogastruridae). *Genus* 16: 1-5.
- YOSII, R. 1966. Collembola of Himalaya. *Journal of the College of Arts and Sciences Chiba University* 4: 461-531.
- YOSII, R. 1971. Collembola of Khumbu Himal. *In: Khumbu Himal*.





## Nomenclatural note on the genus *Nans* (Ostariophysi, Characidae)

Juan Marcos MIRANDE<sup>1</sup>, Gastón AGUILERA<sup>1</sup> &

María de las Mercedes AZPÉLICUETA<sup>2</sup>

<sup>1</sup> Fundación Miguel Lillo, Miguel Lillo 251, 4000 Tucumán, Argentina.

E-mail: mcmirande@tucbbs.com.ar

<sup>2</sup> División Zoología Vertebrados, Facultad de Ciencias Naturales y Museo, Paseo del Bosque, 1900 La Plata, Argentina. E-mail: azpeli@museo.fcnym.unlp.edu.ar

### Nomenclatural note on the genus *Nans* (Ostariophysi, Characidae). -

The generic name *Nans* Mirande, Aguilera & Azpelicueta, 2004 is preoccupied by an annelid. The monotypic fish genus *Nans* is therefore renamed to *Nantis*.

**Keywords:** Characiformes - *Nans* - *Nantis* - homonymy - new name.

*Nantis* nom. nov.

TYPE SPECIES: *Nans indefessus* Mirande, Aguilera & Azpelicueta, 2004.

ETYMOLOGY: *Nantis* is deriving from the latin verb *nare* (to swim) (artificial noun). Gender: masculine.

*Nans indefessus* Mirande, Aguilera & Azpelicueta, 2004 was described as a new genus and species from the upper Río Bermejo basin, Northwestern Argentina. According to Neave (1940) the generic name *Nans* is preoccupied by an annelid (Chamberlin, 1919: 125). In order to clear this homonymy we propose *Nantis* nom. nov. as a new substitute name for the genus *Nans* Mirande, Aguilera & Azpelicueta, 2004.

## ACKNOWLEDGEMENTS

We thank John K. Page who called our attention to this homonymy.

## REFERENCES

- CHAMBERLIN, R. V. 1919. The Annelida Polychaeta. *Memoirs of the Museum of Comparative Zoology, Harvard University* 48: 1-514.
- MIRANDE, J. M., AGUILERA, G. A. & AZPÉLICUETA, M. M. 2004. A new genus and species of small characid (Ostariophysi, Characidae) from the upper rio Bermejo basin, northwestern Argentina. *Revue suisse de Zoologie* 111(4): 715-728.
- NEAVE, S. A. 1940. Nomenclator Zoologicus. A list of the names of genera and subgenera in zoology from the tenth edition of Linnaeus 1758 to the end of 1935. Volume III M-P. *The Zoological Society of London*.



***Taygete sphecophila* (Meyrick) (Lepidoptera; Autostichidae): redescription of the adult, description of the larva and pupa, and impact on *Polistes* wasps (Hymenoptera; Vespidae) nests in the Galapagos Islands**

Bernard LANDRY (BL)<sup>1</sup>, David ADAMSKI (DA)<sup>2</sup>, Patrick SCHMITZ (PS)<sup>3</sup>,  
Christine E. PARENT (CEP)<sup>4</sup> & Lazaro ROQUE-ALBELO (LR)<sup>5</sup>

<sup>1</sup> Muséum d'histoire naturelle, C.P. 6434, 1211 Genève 6, Switzerland.

E-mail: bernard.landry@ville-ge.ch

<sup>2</sup> Department of Entomology, National Museum of Natural History, P.O. Box 37012,  
NHB - E523, Smithsonian Institution, Washington, DC, 20013-7012, USA.

E-mail: dadamski@sel.barc.usda.gov

<sup>3</sup> Muséum d'histoire naturelle, C.P. 6434, 1211 Genève 6, Switzerland.

E-mail: patrick.schmitz@ville-ge.ch

<sup>4</sup> Behavioural Ecology Research Group, Department of Biological Sciences,  
Simon Fraser University, Burnaby, British-Colombia V5A 1S6, Canada.

E-mail: cparent@sfu.ca

<sup>5</sup> Department of Entomology, Charles Darwin Research Station, Casilla 17-01-3891,  
Quito, Ecuador; Biodiversity and Ecological Processes Research Group, Cardiff  
School of Biosciences, Cardiff University, PO Box 915, Cardiff CF10 3TL, United  
Kingdom. E-mail: lazaro@fcdarwin.ec.org

***Taygete sphecophila* (Meyrick) (Lepidoptera; Autostichidae): redescription of the adult, description of the larva and pupa, and impact on *Polistes* wasps (Hymenoptera; Vespidae) nests in the Galapagos Islands.**

- *Taygete sphecophila* (Meyrick) (Lepidoptera; Autostichidae) is reported on the Galapagos Islands. The morphology of the moth, larva, and pupa are described and illustrated in details. Part of the mitochondrial DNA was sequenced and made available on GenBank. The incidence of predation by *T. sphecophila* on nests of *Polistes versicolor* Olivier (Hymenoptera; Vespidae) was measured in four different vegetation zones of Floreana and Santa Cruz Islands. The percentages of infested nests varied greatly (from 13.9% to 66.7% on Floreana and from 20.0 to 100% on Santa Cruz) and no clear ecological trends could be ascertained.

**Keywords:** Micro moths - Autostichidae - *Taygete* - *Polistes* - Galapagos Islands - mitochondrial DNA - larval predation - morphology - ecology.

**INTRODUCTION**

*Taygete* was described by Chambers (1873) to accommodate *Evagora difficilisella* Chambers, 1872 (Nye & Fletcher, 1991). The latter name proved to be a synonym of *T. attributella* (Walker, 1864). The genus appears to be restricted to the

New World. Becker (1984) lists 13 names in this genus for the Neotropical fauna while Hodges (1983) lists six species for the North American fauna, including five that are stated to be misplaced in this genus. BL's examination of the type specimens of the Neotropical species at the Natural History Museum, London, points to the possibility that only *T. sphecephila* (Meyrick, 1936) is congeneric with *T. attributella* in this region. However, the types of *Epithectis consociata* Meyrick, *E. notospila* Meyrick, and *E. altivola* Meyrick have lost their abdomen and cannot be assigned to genus, and the type of *E. lasciva* Walsingham, deposited in the USNM, Washington, could not be found.

*Taygete* Chambers was considered to belong to the Gelechiidae until Landry (2002) moved it to the Autostichidae, Symmocinae sensu Hodges (1998). *Taygete sphecephila* was described from three specimens bred in Trinidad from "bottom of cells of the Hymenopteron *Polistes canadensis*" (Meyrick, 1936). The moth and male genitalia were later illustrated with black and white photography by Clarke (1969). On the Galapagos Islands moths of *T. sphecephila* were first collected in 1989 by BL, but the species probably arrived earlier within nests of *Polistes versicolor* Olivier (Vespidae).

The purposes of this paper are to redescribe and illustrate the moth of *T. sphecephila*, to describe and illustrate the larva and pupa, to present part of its mitochondrial DNA, and to report on a few aspects of its biology, particularly with regard to the incidence of damage to *P. versicolor* nests by larvae.

## MATERIAL AND METHODS

Moths of *T. sphecephila* were first collected at night with a mercury vapor light set in front of a white sheet and powered by a small generator, and with an ultra-violet lamp powered by a battery. Other adult specimens were reared from contained nests of *Polistes versicolor*. Immature stages were found by dissecting *Polistes* nests and by exposing them to the sun, which causes larvae to exit nests and run away from them (Fig. 2).

Specimens are deposited in the Charles Darwin Research Station (CDRS), Santa Cruz, Galapagos, Ecuador; the Canadian national Collection of Insects (CNC), Ottawa, Ontario, Canada; the United States National Museum of Natural History, Washington, D.C., U.S.A. (USNM), and the Muséum d'histoire naturelle (MHNG), Geneva, Switzerland.

For the study of specimens using electron microscopy, larvae and pupae were first rinsed several times in water, cleaned in 10% EtOH with a camel hairbrush, and then dehydrated in EtOH as follows: 10% EtOH for 15 minutes, 20% for 15 minutes, 40% for 15 minutes, 70% for 1/2 hour, 90% for 1/2 hour, and 100% for 1/2 hour each in two separate baths. After dehydration, specimens were critical-point dried using a Tousimis critical point dryer, mounted on stubs, and coated with gold-palladium (40-60%) using a Cressington sputter coater. The ultrastructure of the larvae and pupa was studied with an Amray scanning electron microscope.

Gross morphological observations and measurements of the larvae and pupae were made using a dissecting microscope (reflected light) with a calibrated micrometer.





1



2

FIGS 1-2

1, *Taygete sphecophila*, female; 2, part of an abandoned nest of *Polistes versicolor* exposed to the sun with at least 8 larvae of *Taygete sphecophila* exiting from it.

Maps of the larval chaetotaxy were initially drawn using a WILD dissecting microscope with a camera lucida attachment. Terminology for chaetotaxy follows Stehr (1987).

In order to certify that the larvae corresponded to the adults found we sequenced a fragment of the mitochondrial gene Cytochrome oxidase I (COI) of both. Whole genomic DNA was extracted using the Nucleospin kit (Macherey-Nagel). The COI gene was amplified by PCR with two primers: k698 (5'-TACAATTTATCGCC-TAAACTTCAGCC-3'), and Pat2 (5'-TCCATTACATATAATCTGCCATATTAG-3'). The thermal profile started with an initial denaturation at 95°C for 5 min, followed by 35 cycles at 94°C for 30 s, 47°C for 30 s, and 72°C for 1 min 30 s, and a final step at 72°C for 10 min. The purified PCR product was sequenced in both directions using fluorescent dye terminators in an ABI 377 automated sequencer. The sequence is available from GenBank (Accession No. DQ309437).

In order to determine the distribution and the density of *Taygete sphecochila* as predator on *Polistes versicolor* nests, several study sites were selected in four of the vegetation zones of Santa Cruz and Floreana Islands. In each vegetation zone a series of quadrats of 10 m x 10 m were made at random, and the number of active and inactive nests of *Polistes versicolor* were counted. The delimitation of vegetation zones was based on vegetation composition (Wiggins & Porter, 1971). Nests were found by visually searching the study sites. In addition, nests found in and near Puerto Ayora, a small town located on the littoral and arid zones on the south coast of Santa Cruz Island, were included in the study. The presence of *T. sphecochila* in *Polistes* nests was determined by the presence of little holes on the back of the nests (Fig. 2) and distinctive breaches on the capped cells normally occupied by wasp pupae. In 1999, nests of *Polistes versicolor* were monitored weekly in the area of Puerto Ayora, and nests that were abandoned after being infested by *T. sphecochila* were collected during that period of time. Some adults of *T. sphecochila* that emerged from these nests were preserved dry for taxonomic identification. The ecological observations were made between April and August 1999, February and April 2002 and 2003 on Santa Cruz Island, and between April and August 1999 on Floreana Island. To test for ecological or insular trends in the frequency of parasitism of *P. versicolor* nests by *T. sphecochila*, we performed a G-test for goodness of fit (Sokal & Rohlf, 1995) on each island dataset using the proportion of *P. versicolor* nests in a given zone to infer the expected frequency of parasitism by *T. sphecochila*.

## TAXONOMIC TREATMENT

### *Taygete sphecochila* (Meyrick)

*Epithectis sphecochila* Meyrick, 1936: 624; Gaede, 1937: 113; Clarke, 1955: 290; Clarke, 1969: 63, pl. 31 figs 4-4b; Makino, 1985: 25; Yamane, 1996: 85.

*Taygete sphecochila* (Meyrick); Becker, 1984: 47; Landry, 1999: 68; Landry, 2002: 818-819.

MATERIAL EXAMINED FOR MORPHOLOGICAL WORK: Moths (13 specimens from the Galapagos Islands, Ecuador): SANTA CRUZ: 1 ♀, C[harles] D[arwin] R[esearch] S[tation], arid zone, 19.i.1989, M[ercury] V[apor] L[amp] (B. Landry); 4 ♀ (two dissected with genitalia on slides CNC MIC 4586 & BL 1196, the latter with right wings on slide BL 1313), CDRS, arid zone, 3.ii.1989, MVL (B. Landry); 2 ♂ (one dissected, slide BL 1126), Barranco, ex larva en nido *Polistes versicolor*, 8.ii.1999 (L. Roque, No. 99.20); 1 ♀, NNW Bella Vista, GPS: 225 m elev., S 00° 41.293', W 090° 19.665', 18.ii.2005, u[ltra] v[iolet] l[ight] (B. Landry, P. Schmitz); 1 ♀ (dissected, slide BL 1195), 2 km W Bella Vista, 27.ii.1989, MVL (B. Landry); 1 ♀, casa L. Roque-Albelo & V. Cruz, GPS: 137 m elev., S 00° 42.595', W 090° 19.196', 27.ii.2005, uvl (B.

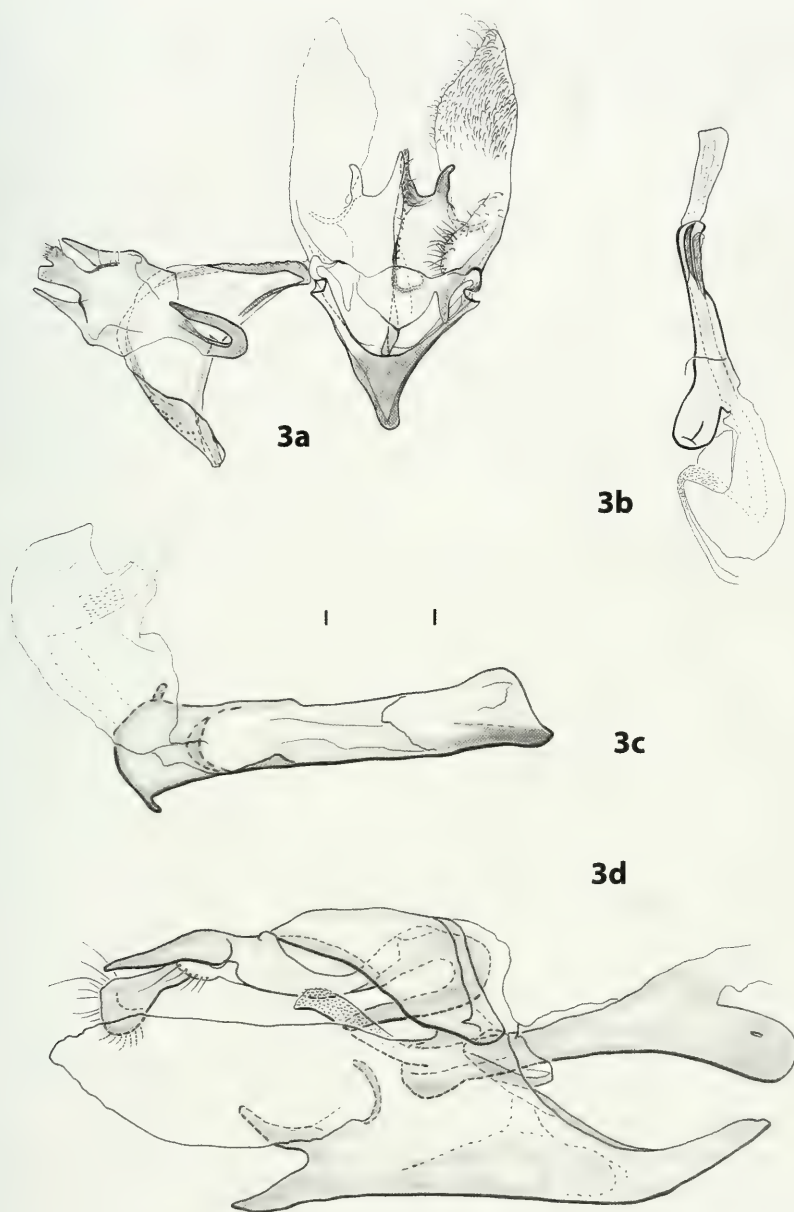


FIG. 3

*Taygete sphecophila*, male genitalia (sizes not proportionate). 3a, dorsal view of valvae + vinculum + juxta and ventral view of tegumen + uncus + gnathos detached on right side and spread on left side, phallus removed, setae shown on right side only; 3b, side view of phallus with vesica everted; 3c, dorsal view of phallus, vesica inverted, scale = 0.1 mm; 3d, lateral view of whole genitalia.



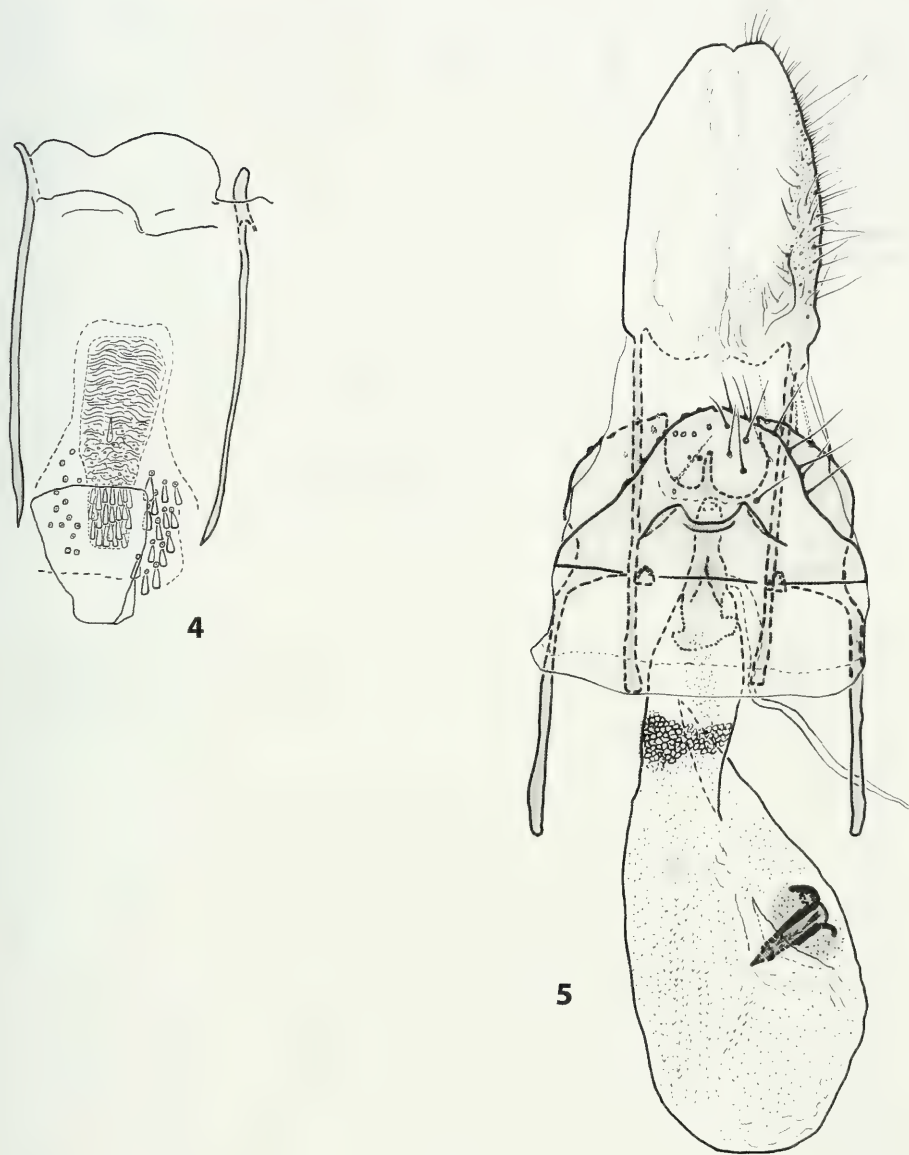
Landry); 2 ♂ (dissected, slides BL 1208 & 1209), émergé d'un nid de Polistes, 1999 (C. Parent). SAN CRISTOBAL: 1 ♂, antiguo botadero, ca. 4 km SE P[uer]to Baquerizo, GPS: 169 m elev., S 00° 54.800', W 089° 34.574', 22.ii.2005, uvl (B. Landry).

Larvae (166 specimens) and pupae (10 specimens) collected on Santa Cruz by P. Schmitz in 2004 and 2005.

**DIAGNOSIS:** The presence in males of this species of a corematal organ at the base of the abdomen (Fig. 4) and a trifurcated uncus (Fig. 3a) are excellent diagnostic features with regards to the rest of the Galapagos fauna. Males of *Galagete* Landry are the only other Galapagos moths to share a corematal organ, but their uncus is made of a single projection. In females the shape of segment VIII (Fig. 5), especially dorsally, will separate *T. sphecephila* from any other species in the Galapagos and probably the rest of its range. On the archipelago, some species of *Galagete* Landry (2002) or Gelechiidae may appear superficially similar, especially because they share a similarly shaped hindwing, a similar wingspan, upturned labial palpi, and scales on the proboscis basally, but the forewing markings of *T. sphecephila* (Fig. 1) are unique among these groups.

**REDESCRIPTION:** General appearance of moth greyish brown with dark brown markings on forewing (Fig. 1); scales usually dark brown at their base and paler apically. Head scales longer laterally and directed medially and ventrally, except on occiput, directed medially and dorsally. Ocellus and chaetosema absent. Labial palpus gently curving upward, darker brown laterally than medially, with white rings of scales mostly at apex of segments; segments II and III shorter together than segment I. Antenna mostly greyish brown, darker brown toward base; flagellomeres in both sexes simple and with erect scales ventrally from about middle of flagellum. Thorax concolorous with head, sometimes darker brown at base. Foreleg mostly dark brown, with beige scales at apex of tarsomere I and on all of tarsomere V. Midleg mostly dark brown laterally, with paler scales at apex of tarsomeres I and II, and on all of tarsomere V, uniformly beige medially on femur and tibia, also with short tuft of dark brown scales dorsally on basal half of tibia. Hindleg paler than other legs, with some dark brown laterally on femur and tibia, mostly dark brown on tibial spines and at base of tarsomeres I-IV, also with tuft of long dirty white scales on dorsal margin of tibia. Wingspan: 7.5-9.0 mm. Forewing mostly greyish brown, with three dark brown triangular markings on costa, largest marking at base, reaching inner margin, smallest submedially situated, barely reaching cell, third marking large, reaching middle of wing; with dark brown scaling also at apex and as 1-3 small patches of 10 scales or less below postmedian costal marking; also with variable amounts of yellowish-orange to rusty-brown scales usually within basal dark brown marking, below postmedian marking, and toward apex; fringe dark brown at apex, more greyish brown elsewhere. Hindwing greyish brown without markings, with concolorous fringe. Wing venation (based on slide BL 1313, female) (Fig. 6): Forewing Sc to about 2/5 wing length; R1 from about middle of cell; R2 and R3 separate, both from before upper angle of cell; R4, R5, and M1 from upper angle of cell, connected, R4 and R5 directed toward costa before apex, M1 directed toward outer margin below apex; M2 and M3 separate, M2 from lower angle of cell, M3 from shortly before lower angle of cell; CuA1 and CuA2 separate, both from shortly before lower angle of cell; CuP absent; cell a little more than half





FIGS 4-5

*Taygete sphecophila*. 4, ventral view of first abdominal segment; 5, ventral view of female genitalia, setae shown on right side only.

wing length; A1 and A2 joined at about  $1/5$  their lengths. Female forewing retinaculum consisting of anteriorly directed scales at base of cubital stem and posteriorly directed scales at base of Sc. Hindwing Sc closely following costa, reaching it at about  $3/5$  wing length; Rs connected with M1 after upper angle of cell, Rs reaching costa at about  $4/5$

wing length, M1 directed toward apex; M2 from slightly above lower angle of cell, reaching outer margin below middle; M3 and CuA1 connected for about 1/2 their lengths after lower angle of cell, M3 to tornus, CuA1 to inner margin shortly before tornus; CuA2 from about 2/3 cell to inner margin at 7/10; CuP and anal veins indistinct; apex distinctly produced; outer margin distinctly concave; female frenulum with 2 acanthae. Abdomen dorsally mostly dark greyish brown, with dirty white scales at apex of all segments except last; ventrally dark brown on each side of large dirty white band except for last segment, mostly concolorous, greyish brown; male first abdominal segment (Fig. 4) ventrally with an invaginated pouch containing a membranous structure bearing scales (see Note below).

Male genitalia (Fig. 3). Uncus moderately long, with pair of fixed lateral, pointed and gently tapering glabrous projections; also with movable median projection, slightly longer than lateral projections, enlarged at apex and bifid, with each end bulbous and setose, also slightly setose at base laterally. Gnathos a long curved rod pointing posteriorly, apically more heavily sclerotized, tapered, glabrous, and rounded. Tegumen broad medially, with moderately narrow pedunculi. Valva with unsclerotized setose cucullus, tapering, rounded apically, with slightly sclerotized setose ridge at base on inner side, also with medium sized apodemes directed anteriorly from base of costa; sacculus with pair of short, narrow, setose, and apically rounded projections, dorsal projection curved and directed dorsally, ventral one straight and directed posteriorly. Vinculum narrow, slightly projected anteriorly and upturned. Juxta poorly developed, small, better sclerotized at posterior edge around phallus. Phallus (= aedeagus of authors, but see Kristensen, 2003) narrow, with shaft flattened dorsoventrally beyond middle, better sclerotized on left side in narrow band, slightly upturned apically; coecum penis medium-sized with pair of very small peduncles laterally; vesica with minute scobination.

Female genitalia (Fig. 5). Papillae anales large and long, moderately setose, sclerotized dorsally and laterally at base. Posterior apophyses slightly curved apically, slightly longer than papillae. Tergum VIII well sclerotized, with few long setae especially on margin, with deep rounded concavity in middle apically; middle of concavity with posteriorly directed projection variable in length and bearing two setae. Anterior apophyses straight, slightly enlarged apically, about as long as papillae. Sternum VIII with apical margin bell shaped, well sclerotized, with few long setae mostly posteriorly along margin and midventrally. Intersegmental membrane between sternites VII and VIII slightly sclerotized on each side of midventral line and with pair of short projections inside body at apical margin. Ostium bursae in middle of sternite VIII, ventrally protected by slightly protruding crescent of sclerotization. Ductus bursae short, gradually enlarging, basal half well sclerotized, distal half spiculose and with wrinkles patterned like brood cells in bee hive. Corpus bursae slightly longer than wide, spiculose, with one large, spiny, curved, and pointed cornutus; latter set in small sclerotized patch with pair of bumps on each side of its base.

DESCRIPTION OF THE LARVA AND PUPA: Larva. (Figs 7-17): Length 5.0-8.2 mm ( $n = 72$ ), < 5.0 mm ( $n = 94$ ). Body pale gray, textured with microconvolutions; head capsule amber; prothoracic shield amber, gradually darkening posteriorly; pinacula pale brown; anal plate pale amber; setae with widened, circular, and slightly raised

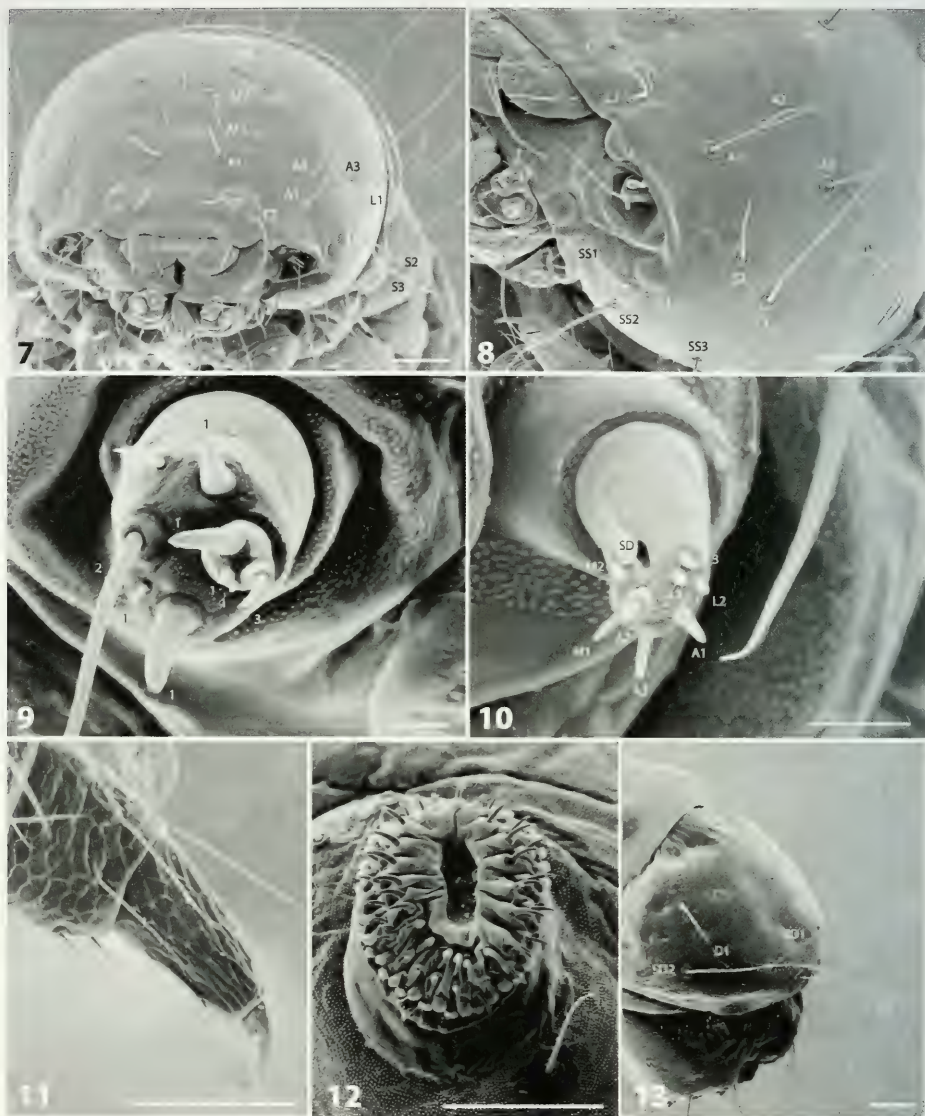


FIG. 6

Wing venation of *Taygete sphecophila*.

sockets. Head (Figs 7-10, 17): hypognathous, textured with slightly raised, confluent, polygonal ridges except on area between adfrontal sclerites (Figs 7-8); adfrontal sclerites widened distally, frontal setae about equal in length, AF2 above apex of frons, AF1 below; F1 slightly closer to AF1 than to C1; C2 at least 2 1/2 times longer than C1; clypeus with 6 pairs of setae, 3 pairs on medial half, 3 on distal half; mandible angular (Fig. 17), shallowly notched subapically forming small apical dentition, bearing pair of subequal setae on outer surface near condyle, and with 1 large dentition on inner surface; sensilla types and arrangement on antenna (Fig. 9) and on maxillary palpi (Fig. 10) similar to those of other Gelechioidea studied by Adamski & Brown (1987), Adamski (1999), Adamski & Pellmyr (2003), Landry & Adamski (2004), and Wagner *et al.* (2004), and other Lepidoptera studied by Adamski & Brown (2001), Albert (1980), Avé (1981), Grimes & Neunzig (1986a, b), and Schoonhoven & Dethier (1966). Three stemmata in genal area, 1 approximate pair above antenna, and 1 stemma below antenna; substemmatal setae about equal in length, arranged as in Fig. 8; S3 and S1 elongate and about equal in length, S2 short; S3 lateroventral to S2, S2 approximate to stemma 3, and S1 approximate to stemma 5 (stemmata 1, 2, and 6 absent); A-group setae above gena, mesal to L1; P1 dorsolateral to AF2, P2 dorsomesal to P1. Thorax (Figs 11, 14): T1 with L-group trisetose, on large pinaculum extending beneath and posterior of spiracle; setae anterior to spiracle; L1 approximate and posteroventral to L2, about 2 1/2 times lengths of L2 and L3; SV-group setae on anterior part of elongate pinaculum; SV1 about 1/3 longer than SV2; coxae nearly touching, V1s very approximate (not shown); segments of leg textured with slightly elongate ridges, many produced distally into hairlike spines, claw single (Fig. 11); shield with SD1 slightly posterior to and about 1/3 longer than XD2 and XD1; XD2, XD1, D1, and SD2 about





FIGS 7-13

Scanning electron micrographs of larva of *Taygete sphecephila*. 7, Frontolateral view of head capsule, scale = 100  $\mu$ ; 8, Ventrolateral view of head capsule, scale = 100  $\mu$ ; 9, Sensilla of antenna: 1 = sensilla basiconica, 2 = sensillum chaetica, 3 = sensillum styloconicum, 4 = sensillum trichodeum, scale = 10  $\mu$ ; 10, Sensilla of maxillary palpus: A2 = sensillum styloconicum, A1, A3, M1-2, L1-3 = sensilla basiconica, SD = sensillum digitiform, scale = 10  $\mu$ ; 11, Distal portion of left prothoracic leg showing claw, scale = 10  $\mu$ ; 12, Left proleg on A4, scale = 100  $\mu$ ; 13, Anal plate of A10, scale = 100  $\mu$ .

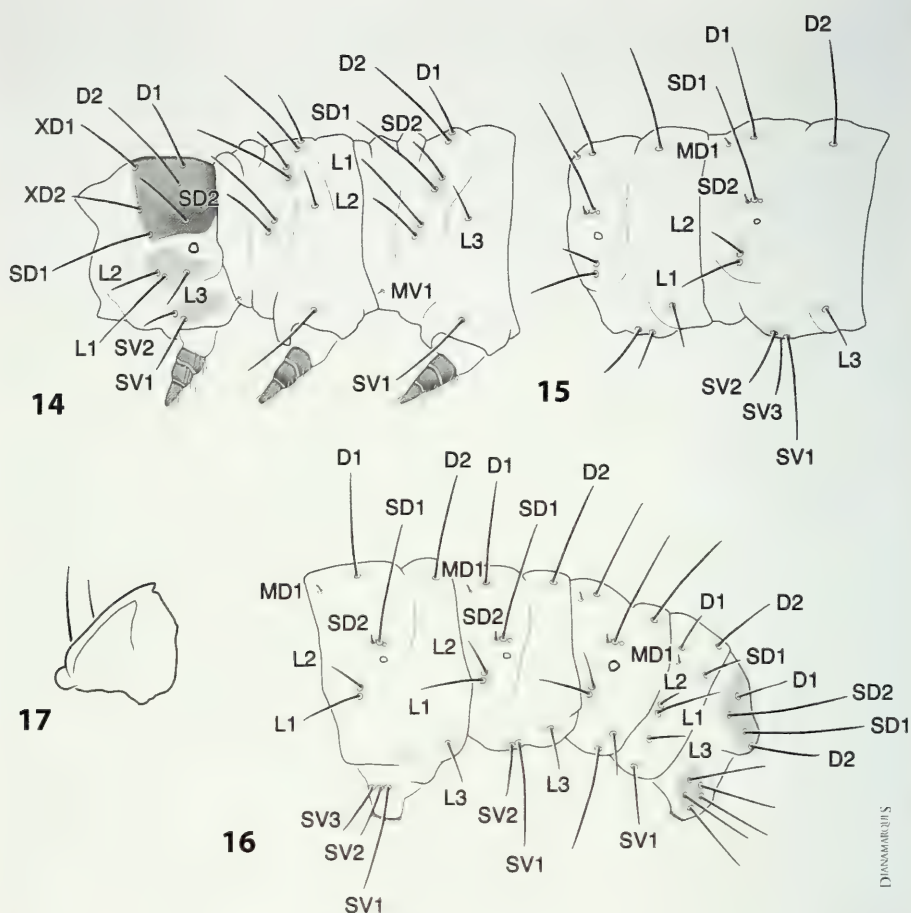


equal in lengths, XD2 about twice distance from XD1 than from SD1; D1 in straight line with XD1, slightly posterior to SD2 and D2; D2 about same length as SD1, in straight line with SD2. T2-T3 (Fig. 14): D2 about 2 times length of D1, both on small pinaculum; SD1 about 2 times length of SD2, both on small pinaculum; L1 about 1/3 longer than L2, both on small pinaculum, L3 slightly shorter than L2, posterior to or in vertical line with SV1; MV1 on anterior margin between T2-T3, slightly above SV1 (hard to see); V1s on T2-T3 about equal distance apart, at least 4 times distance between V1s on T1. Abdomen (Figs 12, 13, 15, 16): A1-A2 (Fig. 15): D2 and D1 equal in lengths or D2 slightly longer, MD1 on anterior part of segment anteroventral to D1; SD1 above spiracle, about 1/3 longer than D2, with minute SD2 (anterior part of pinaculum); small opening on ventroposterior margin of pinaculum bearing SD1 and SD2; spiracle on A1 slightly larger than those on A2-A7; L1 2 times length of L2, both on same pinaculum, slightly anterior of spiracle; L3 about same length as L2, anterior to, in vertical line with, or posterior to D2; SV-group bisetose on A1, trisetose on A2, on same pinaculum; V1s equal distance apart (not shown). A3-A10 (Figs 12, 13, 16): A3-A6 with 4 pairs of protuberant prolegs, crochets biordinal, in circle (Fig. 12); setae as above; A7 as above except, SV-group bisetose and on same pinaculum; A8 as above except with spiracle slightly larger than on previous segments and SV-group unisetose; A9 with D2 about 2-2 1/2 times longer than D1; D1 anterior to D2 and SD1, equidistant to both setae; SD1 about same length as D1; L-group setae slightly anterior to D1; L1 about 3 times length of L2, on same pinaculum; L3 slightly longer than L2; SV1 slightly shorter than L1; V1s as previous segments; A10 (Figs 13, 16): anal plate with SD2 and SD1 equal in lengths, about twice length of D2; D1 slightly shorter than D2; crochets of proleg biordinal, in semicircle, gradually shortened mesally and laterally.

Pupa. (Figs 18-21): Length 3.6-4.6 (n = 10): amber, smooth, spiracles protuberant; all dorsal setae apically hooked except long seta associated with axillary tubercle (Figs 19-20). Sclerites of antennae annulated, widely separated anteriorly, gradually convergent from beyond basal 1/3 of sclerites of maxillae, fused for short distance beyond distal apices of sclerites of maxillae, gradually divergent posteriorly, exposing distal part of sclerites of hindlegs; sclerites of midleg not fused distally; paired nodular scars of prolegs on A5-A6 (Fig. 18); A6-A10 fused, rotating as unit; cremaster dorsolaterally flattened, trapezoidal basally, extending posterolaterally into 2 slightly divergent and elongate spine-like processes (Fig. 21).

DISTRIBUTION AND PHENOLOGY: The species was described from Trinidad (Meyrick, 1936) and never mentioned from anywhere else subsequently. In the Galapagos Islands it has been found on Floreana (from the littoral to the humid zones), San Cristobal (in the arid zone), and Santa Cruz (from the littoral to the humid zones). In the Galapagos we have collected live moths of this species in January, February, March, April, September, November, and December.

NOTES: Preliminary phylogenetic analyses, both morphological and molecular, support the placement of *Taygete sphecophila* within Autostichidae (PS, unpublished data). For example, Kaila's (2004) matrix was reanalyzed with *T. sphecophila* data, and the species clusters in Kaila's autostichid assemblage with *Galagete* Landry.



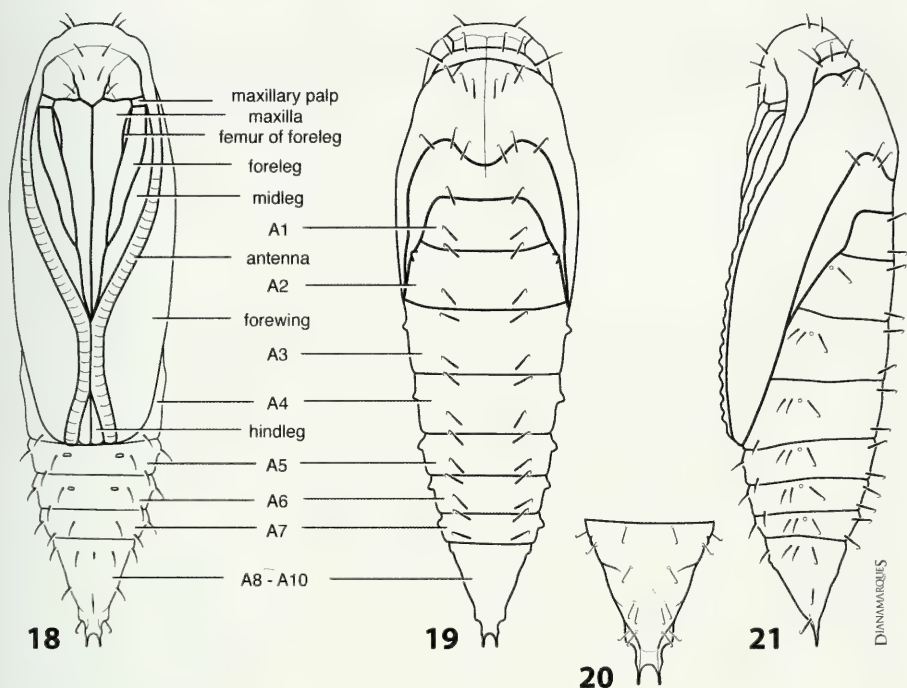
FIGS 14-17

Larva of *Taygete sphecophila*. 14, Chaetotaxy of thorax; 15, Chaetotaxy of abdominal segments 1-2; 16, Chaetotaxy of abdominal segments 6-10; 17, Mandible.

A comparison of a 1283 base pairs fragment (consisting of most of the COI gene except the first 254 base pairs) sequenced for a larva and an adult of *Taygete sphecophila* showed no substitution, which clearly indicates conspecificity.

The larva has only three stemmata, a condition that is highly unusual in Gelechioidea and that may be due to the unique host relationship.

It proved impossible to evaginate the ventro-abdominal pouch (Fig. 4) in several male specimens of this species. However, BL was able to evaginate this core-matal organ from a specimen of *Taygete attributella* (Walker). The organ consists of a narrow membranous tube, almost as long as the abdomen, on which narrow scales are connected all around. The membrane of the tube is very thin and the tube collapsed as soon as specimens were transferred to lactic acid for temporary storage. An illustration of this structure for the closely related *Galagete turritella* Landry is provided by Landry (2002: Figs 17, 18).



FIGS 18-21

Pupa of *Taygete sphecophila*. 18, Ventral view; 19, Dorsal view; 20, Segments 8-10; 21, Lateral view.

## ECOLOGICAL STUDY

### PATTERNS OF PREDATION

Although egg-laying was never observed, it is possible that the female moths lay their eggs within the pupal cells of *P. versicolor* through numerous small holes of 1-2 mm in diameter that we observed on the back of the nests. In a sample of 25 *P. versicolor* nests, the number of *T. sphecophila* moths found per nest varied between 3 and 13. However, 42 *T. sphecophila* larvae were recovered by PS from a rather small nest collected on Santa Cruz in 2004. The food source needed for the development of the moth's larvae are the wasps' pupae which are defenseless because of their isolation in their capped cells. When ready to emerge from the wasp's cell, the moth makes a distinctive breach through the cap covering the top of the cell.

### DISTRIBUTION OF INFESTED NESTS

The level of *T. sphecophila* infestation could only be assessed for nests of *P. versicolor* that were abandoned. A total of 103 such nests were found on the different study sites on Santa Cruz Island between 1999 and 2003, and 141 nests on Floreana Island in 1999. The percentages of nests that presented signs of predation by *T. sphecophila* are given in Table 1, along with the vegetation zones in which they were found.

TABLE 1. Percentage of *Polistes versicolor* nests found in four different vegetation zones of Santa Cruz and Floreana Islands presenting signs of *Taygete sphecophila* predation. Number of nests per sample are in parentheses.

Vegetation Zone	% of nests with <i>T. sphecophila</i> predation	
	Santa Cruz Island	Floreana Island
Littoral	35.3 (n=17)	40.0 (n=5)
Arid	43.0 (n=79)	13.9 (n=101)
Transition	20.0 (n=5)	66.7 (n=6)
Humid	100.0 (n=2)	51.7 (n=29)

On Santa Cruz island the arid zone was the area of highest abundance of nests. This result is similar to that obtained by Roque-Albelo & Causton (1999) for abundance of adult foragers. The percentages of infestation varied between zones (Table 1). However, very few nests were collected in the littoral, transition, and humid zones. Nests of *P. versicolor* were again more common in the arid zone of Floreana. However, only 13.9% of them were infested by *T. sphecophila* in this zone. In contrast to Santa Cruz, on Floreana nests also were abundant in the humid zone, where 51.7 % of them were infested.

The results of the G-test for goodness of fit allow us to test for ecological trend in nest infestation according to vegetation zonation. The proportion of parasitism in *Polistes versicolor* nests in the four vegetation zones on Santa Cruz Island does not show deviation from the expected (based on the proportion of *P. versicolor* nests found in each vegetation zone;  $G = 4.806$ ,  $df = 3$ ,  $P > 0.05$ ). However, the situation on Floreana Island appears different as *P. versicolor* nests found in the arid zone are infested by *T. sphecophila* less than expected, and nests found in the transition and humid zones are infested more than expected ( $G = 15.482$ ,  $df = 3$ ,  $P < 0.01$ ).

## DISCUSSION

Different factors, including climatic conditions, infestation by nest scavengers and parasitoids, and predation affect the wasp colony cycle (Yamane, 1996). Across its range of distribution, from Costa Rica to Southern Argentina, *P. versicolor* seems to prefer dry forest habitats (Richards, 1978). Data from previous studies suggest that in the Galapagos the wasps are more abundant in the arid zone of the islands (Roque-Albelo & Causton, 1999; Lasso, 1997). This preference in distribution could be associated with climatic conditions (Parent, 2000). In the Galapagos the higher zones of the islands are cooler and receive more rainfall than lower zones, particularly on the southern slopes, and this factor probably affects nest development. Collection data of *T. sphecophila* suggest a similar pattern of distribution. Most moth specimens were collected in the dryer zones of the islands suggesting a close correlation with nest abundance.

On Santa Cruz Island the occurrence of *T. sphecophila* in different vegetation zones is a reflection of the frequency of *P. versicolor* nests. However, *T. sphecophila* seems to be more abundant than expected in the transition and humid zones of Floreana Island and less frequent in the arid zone. Therefore, *T. sphecophila*'s occurrence on Floreana Island is not strictly a reflection of the abundance of *P. versicolor* nests,



suggesting that other ecological or climatic factors might influence its distribution. It is not clear why there is such a difference between Floreana and Santa Cruz islands, but one possible hypothesis is that *T. sphecochila* has colonized these two islands at different points in time, so that populations on one of the island have had more time to adapt to the island's ecological and climatic context.

*Polistes* nests, as in many other social wasps, are scavenged and parasitized by various insects including more than 11 moth species from four families (Makino, 1985). Only *Taygete sphecochila* was found in the Galapagos, where the species apparently prefers to attack large nests, and all infested nests collected were large enough to presume that they were in an advanced stage of the reproductive phase. If predation by *T. sphecochila* is restricted to this stage of the wasp colonies the probabilities for this moth species to be an effective agent of biological control are reduced. These results support the idea of Miyano (1980) that parasitic and scavenging Lepidoptera reduce notably the colony's productivity but are not thought to be a direct cause of colony failure. However, the possibility to use *T. sphecochila* as a biological control agent against *P. versicolor* needs to be evaluated.

We believe that the first individuals of *Taygete sphecochila* probably arrived within a nest of *P. versicolor* built on some human-made structure that would have traveled by boat from the continent. It is actually quite possible that both animals arrived together on the Galapagos. The wasp was first detected in 1988 on Floreana, and is thought to have arrived with a shipment of bananas (Abedrabbo, 1991), but Eduardo Vilema, resident of Santa Cruz, says that he first saw a nest of *Polistes versicolor* near Bella Vista, on Santa Cruz, in 1984 or 1985 (pers. comm. to BL in 2004). And we think it unlikely that the wasps came on banana regimes as they are not known to build their nests there.

#### ACKNOWLEDGEMENTS

BL would like to thank the authorities of the CDRS and Galapagos National Park Service (GNPS) for providing authorizations and logistical support for sampling micro moths in 1989, 1992, 2002, 2004, and 2005. The first two expeditions were organized by Stewart B. Peck, Carleton University, Ottawa, and benefited from financial support of the National Sciences and Engineering Council of Canada. Professor Peck, as well as Bradley J. Sinclair and several others were excellent field companions. BL is also grateful to Jean-François Landry, Agriculture & Agri-Food Canada, Ottawa, for providing lab space, equipment and technical support in 1999-2000. We are thankful to curator Kevin Tuck of the Natural History Museum, London, for his kind help to BL in London and for providing information on references regarding *T. sphecochila* and on specimens of other species. Financial support for BL's investigations in London in 2000 were provided by the Galapagos Conservation Trust, United Kingdom, and the Charles Darwin Foundation.

PS would like to thank the CDRS and GNPS for allowing field work and providing logistical support in the Galapagos in 2004 and 2005. Research funds to PS were provided by the A. Lombard Foundation, the E. & L. Schmidheiny Foundation, the Swiss Academy of Sciences, and the Department of cultural affairs of the city of Geneva.

CEP would like to thank the CDRS and GNPS for providing logistical support and required permits to conduct field work in Galapagos in 1999. Research funds to CEP were provided by CIDA, the Canadian International Development Agency.

DA thanks Diana Marques, scientific illustrator, for the illustrations (Figs 14-21) of the larva and pupa and the digital production of the plates, and Scott D. Whittaker, Manager of the Scanning Electron Microscopy Laboratory, Smithsonian Institution, Washington, DC, for the help with the preparation of the larval specimens for study.

LR thanks Henry Herrera of CDRS for his help in the field and in the lab.

Finally, we are grateful to Lauri Kaila and Klaus Sattler for reviewing the manuscript.

## REFERENCES

- ABEDRABBO, S. 1991. Nueva avispa introducida en las islas. *Carta Informativa* 31: 4.
- ADAMSKI, D. 1999. *Blastobasis graminea*, new species (Lepidoptera: Gelechioidea: Coleophoridae: Blastobasinae): A stem borer of sugar cane in Colombia and Venezuela. *Proceedings of the Entomological Society of Washington* 101: 164-174.
- ADAMSKI, D. & BROWN, R. L. 1987. A new Nearctic *Glyphidocera*, with descriptions of all stages (Lepidoptera: Blastobasidae: Symmocinae). *Proceedings of the Entomological Society of Washington* 89: 329-343.
- ADAMSKI, D. & BROWN, J. W. 2001. Systematic review of the *Ecdytolopha* group of genera (Lepidoptera: Tortricidae: Grapholitini). *Entomologica Scandinavica, Suppl.* 58: 1-86.
- ADAMSKI, D. & PELLMYR, O. 2003. Immature stages and redescription of *Blastobasis yuccae-colella* Dietz (Lepidoptera: Gelechioidea: Coleophoridae: Blastobasini), with notes on its biology. *Proceedings of the Entomological Society of Washington* 105: 388-396.
- ALBERT, P. J. 1980. Morphology and innervation of mouthpart sensilla in larvae of the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). *Canadian Journal of Zoology* 58: 842-851.
- AVÉ, D. A. 1981. Induction of changes in the gustatory response by individual secondary plant compounds in larvae of *Heliothis zea* (Boddie) (Lepidoptera, Noctuidae). *Ph.D. dissertation, Department of Entomology, Mississippi State University*, 89 pp., 4 tables, 37 figs.
- BECKER, V. O. 1984. Gelechiidae (pp. 44-53). In: HEPPNER, J. B. (ed.). Atlas of Neotropical Lepidoptera, Checklist: Part 1, Micropterigoidea - Immoidea. *Dr. W. Junk Publishers, The Hague*, xxvii + 112 pp.
- CHAMBERS, V. T. 1873. Micro-Lepidoptera. *The Canadian Entomologist* 5: 221-232.
- CLARKE, J. F. G. 1955. Catalogue of the Type Specimens of Microlepidoptera in the British Museum (Natural History) described by Edward Meyrick. Volume 1. *Trustees of the British Museum, London*, vii + 332 pp.
- CLARKE, J. F. G. 1969. Catalogue of the Type Specimens of Microlepidoptera in the British Museum (Natural History) described by Edward Meyrick. Volume 7. *Trustees of the British Museum (Natural History), London*, 531 pages.
- GAEDE, M. 1937. Familia: Gelechiidae (pp. 1-630). In: WAGNER, H., STRAND, E. & BRYK, F. (eds). Lepidopterorum Catalogus, part 79, Vol. IV. *Dr. W. Junk, Berlin*.
- GRIMES, L. R. & NEUNZIG, H. H. 1986a. Morphological survey of the maxillae in last-stage larvae of the suborder Ditrysia (Lepidoptera): Palpi. *Annals of the Entomological Society of America* 79: 491-509.
- GRIMES, L. R. & NEUNZIG, H. H. 1986b. Morphological survey of the maxillae in last-stage larvae of the suborder Ditrysia (Lepidoptera): Mesal lobes (Laciniogaleae). *Annals of the Entomological Society of America* 79: 510-526.

- HODGES, R. W. 1983. Gelechiidae (pp. 19-25). In: HODGES, R. W. *et al.* (eds). Check List of the Lepidoptera of America North of Mexico. *E. W. Classey Ltd. and the Wedge Entomological Research Foundation, London*, xxiv + 284 pp.
- HODGES, R. W. 1998. The Gelechioidea (pp. 131-158). In: KRISTENSEN, N. P. (ed.). Handbook of Zoology, Lepidoptera, Moths and Butterflies, Vol. 1: Evolution, Systematics, and Biogeography. *Walter de Gruyter, Berlin & New York*, x + 491 pp.
- KAILA, L. 2004. Phylogeny of the superfamily Gelechioidea (Lepidoptera: Ditrysia): an exemplar approach. *Cladistics* 20: 303-340.
- KRISTENSEN, N. P. 2003. Skeleton and muscles: adults (pp. 39-131). In: KRISTENSEN, N. P. (ed.). Handbook of Zoology, Lepidoptera, Moths and Butterflies, Vol. 2: Morphology, Physiology, and Development. *Walter de Gruyter, Berlin & New York*, x + 564 pp.
- LANDRY, B. 1999. Quatre premières mentions de Lépidoptères pour la province de Québec (Opistegidae, Gelechiidae et Tortricidae). *Fabriques* 24: 66-72.
- LANDRY, B. 2002. *Galagete*, a new genus of Autostichidae representing the first case of an extensive radiation of endemic Lepidoptera in the Galápagos Islands. *Revue suisse de Zoologie* 109: 813-868.
- LANDRY, J.-F. & ADAMSKI, D. 2004. A new species of *Nanodacna* Clarke (Lepidoptera: Elachistidae: Agonoxeninae) feeding on the seeds of *Austrocedrus chilensis* (Cupressaceae) in andean Argentina. *Journal of the Lepidopterists' Society* 58: 100-113.
- LIASSO, T. L. 1997. Ecología e impacto de la avispa introducida (*Polistes versicolor*, Vespidae-Hymenoptera) en las Islas Floreana y Santa Cruz, Galapagos Ecuador. *B.Sc. Thesis, Universidad Central del Ecuador, Quito*, 211 pp.
- MAKINO, S. 1985. List of parasitoides [sic] of Polistine wasps. *Sphecos* 10: 19-25.
- MEYRICK, E. 1936. *Exotic Microlepidoptera* 4: 609-642.
- MIYANO, S. 1980 Life tables of colonies of workers in a paper wasp, *Polistes chinensis antennalis*, in central Japan (Hymenoptera: Vespidae). *Research in Population Ecology* 22: 69-88.
- NYE, I. W. B. & FLETCHER, D. S. 1991. The generic names of moths of the World. Volume 6. Microlepidoptera. *Natural History Museum Publications, London*, xxix + 368 pp.
- PARENT, C. 2000. Life cycle and ecological impact of *Polistes versicolor versicolor* (Olivier) (Hymenoptera: Vespidae), an introduced predatory wasp on the Galapagos Islands, Ecuador. *M.Sc. Thesis, Carleton University, Ottawa, Canada*, 139 pp.
- RICHARDS, O. W. 1978. The social wasps of the Americas excluding the Vespinae. *Trustees of the British Museum (Natural History), London*, Publication No. 785, vii + 580 pp. + 4 pls.
- ROQUE-ALBELO, L. & CAUSTON, C. 1999. Monitoreo de avispa introducidas en las Islas Galápagos. *Charles Darwin Research Station report*, 12 pp.
- SCHOONHOVEN, L. M. & DETHIER, V. G. 1966. Sensory aspects of host-plant discrimination of Lepidopterous larvae. *Archives néerlandaises de zoologie* 16: 497-530.
- SOKAL, R. R. & ROHLF, F. J. 1995. Biometry (3rd ed.). *W. H. Freeman and Company, New York*, 887 pp.
- STEHR, F. 1987. Cosmopterigidae (Gelechioidea) (pp. 391-392). In: STEHR, F. (ed.). Immature insects, Volume 1. *Kendall/Hunt Publishing Company, Dubuque, Iowa*, 754 pp.
- WAGNER, D. L., ADAMSKI, D. & BROWN, R. L. 2004. A new species of *Mompha* Hbn. from Mississippi (Lepidoptera: Gelechioidea). *Proceedings of the Entomological Society of Washington* 106: 1-18.
- WIGGINS, I. L. & PORTER, D. M. 1971. Flora of the Galápagos Islands. *Stanford University Press, Stanford*, xx + 998 pp.
- YAMANE S. 1996. Ecological factors influencing the colony cycle of *Polistes* wasps (pp. 75-97). In: TURILLAZZY, S. & WEST-EBERHARD, M. J. (eds). Natural History and evolution of paper-wasps. *Oxford University Press*, xiv + 400 pp.





## The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Capitata Part 1

Peter SCHUCHERT

Muséum d'histoire naturelle, CP 6434, CH-1211 Genève 6, Switzerland.

E-mail: Peter.Schuchert@ville-ge.ch

**The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Capitata Part 1.** - This study reviews all European hydrozoan species belonging to the capitate families Acaulidae, Boreohydridae, Candelabridae, Cladocorynidae, Cladonematidae, Margelopsidae, Pennariidae, Protohydridae, and Tricyclusidae. Updated diagnoses for the families and genera are provided and existing taxonomic problems solved or at least outlined. *Candelabrum verrucosum* Bonnevie, 1898 is regarded as a valid species and redescribed based on a new record from Greenland. Although *Spadix purpurea* Gosse, 1853 may be a senior synonym of *Candelabrum cocksii* (Cocks, 1854), the latter is regarded as the valid name, this because the former name has not been used after 1899, while the latter has been widely used [ICZN article 23.9.1.1]. Likewise, two senior synonyms of *Eleutheria claparedii* Hartlaub, 1898 are declared as invalid as they have never been used since their original introduction by Haeckel.

**Keywords:** Marine invertebrates - Cnidaria - Hydrozoa - Anthoathecata - Capitata - descriptions - revision - taxonomy.

### INTRODUCTION

This publication is the second in a series of taxonomic revisions of the European Anthoathecata (=Anthomedusae, Athecata) which was begun with the families Oceanidae and Pachycordylidae (Schuchert, 2004). Although it was initially planned to continue with families of the suborder Filifera, some essential material could not be obtained to complete them in time. Therefore, this second paper presents some families of the suborder Capitata.

Following the suggestions of fellow colleagues, the geographic scope of the fauna under investigation has been somewhat extended to match the territory covered by the European Register of Marine Species (Costello *et al.*, 2001). The new scope now also includes the Azores, Iceland, eastern Greenland, Jan Mayen, the Barents Sea, Svalbard, and Franz Joseph Land. The extension of the geographic scope does not add many species. A single species needs to be added to the families treated in the first paper of this series, namely *Similomerona nematophora* (Antsulevich, 1986). This species is already mentioned and diagnosed in Schuchert (2004), but its type locality was erroneously given as "Kurile Islands". Dr Antsulevich informed me that the

species was described from material originating from the archipelago of Franz Joseph Land, thus falling within the limits of the newly adopted coverage. Furthermore, although the paper was authored by Antsulevich & Polteva (1986), the authorship of the species name is due to Dr Antsulevich alone. Although the genus name *Merona* is an artificial word, its ending is characteristic for the feminine gender, thus requiring a change of the specific epithet to *nematophora*.

The current paper treats several families of the suborder Capitata. The families reviewed here were chosen somewhat arbitrarily and do not form a natural unit, though some are evidently closely related. The selection had to be based on the material available for study. The order of the families as given below has no phylogenetic significance and is only thought to group somewhat similar forms together. For a phylogenetic analysis of these families see Petersen (1990). Molecular phylogenies of some families of Capitata can be found in Collins *et al.* (2005a, and b).

## MATERIAL AND METHODS

For morphological methods see Schuchert (1996; 2004) or Bouillon *et al.* (2004). Where possible, it was attempted to supplement the species descriptions by 16S DNA sequence information. The methods to obtain 16S DNA sequences are described in Schuchert (2005). All sequences have been submitted to the EMBL database under the accession numbers: AM088481, AM088482, AM088483, AM088484, AM088485. The origin and identity of the material used to obtain 16S sequence data are given for each species in the section "Material examined". Some sequences have been determined by other laboratories using material described here (accession numbers AY920796, 18S AY920758, AY787879, AY920762, AY512539). Morphological characters of the Cladonematidae were used for a phylogenetic analysis using the parsimony criterion and the program PAUP\* (Swofford, 2001). Bootstrap replicates were performed 1000 times. Only a subset of all Cladonematidae was used. The members of the genus *Cladonema* are all very similar and well represented by *C. radiatum*. For *Staurocladia*, only those species with known life cycle were used. As out-group taxa, three members of the Corynidae were used (comp. Schuchert, 2001b). Table 1 gives the species names and the characters used and their states.

## ABBREVIATIONS

BMNH	The Natural History Museum, London, England
MHNG	Muséum d'histoire naturelle de Genève, Switzerland
ICZN	International Code of Zoological Nomenclature
IRSN	Institut Royal des Sciences Naturelles de Belgique, Bruxelles
ZMUC	Zoological Museum Copenhagen, Denmark
CI	Consistency index
RI	Retention Index
HI	Homoplasy Index

## TAXONOMIC PART

### FAMILY ACAULIDAE FRASER, 1924

DIAGNOSIS: Solitary hydroids, body divided into basal and distal part. Basal part conical to cylindrical, covered or not by gelatinous perisarc which may form anchoring

filaments. Upper part with few indistinctly capitate tentacles or many capitate tentacles, lowest whorl of capitate tentacles may transform into thick filiform tentacles. Gonophores fixed sporosacs in the lower or middle part of the hydranth. Sometimes asexual reproduction by transverse fission.

REMARKS: The name Acaulidae was proposed by Fraser (1924) and this spelling was used by all subsequent authors. According to the ICZN [article 29.3.1.1] there is thus no need to change it to the formally correct Acaulididae.

According to Bouillon (1985), this family contains two genera: *Acaulis* Stimpson, 1854 and *Acauloides* Bouillon, 1965. Petersen (1990) also included the genus *Boreohydra* Westblad, 1937 in the Acaulidae, while Bouillon (1985) kept *Boreohydra* in a separate family Boreohydridae, this together with the genus *Protohydra*. A third genus was later added to the Acaulidae by Thomas *et al.* (1995): *Cryptohydra*. The discovery of *Cryptohydra* narrowed the gap of the Acaulidae to the genus *Protohydra* – and thus Boreohydridae – to a degree that any subdivision now appears entirely arbitrary. The proximity of both families is further emphasized if the nematocyst warts on the body of *Boreohydra* are regarded as reduced capitate tentacles (Calder, 1974). It is thus tempting to fuse both families, but this should only happen in the framework of a broader analysis and discussion and the phylogenetic relationships. The Acaulidae and Boreohydridae have also many similarities with the Candelabridae and Tricyclusidae, and the demarcations are equally arbitrary. Because a phylogenetic analysis based on morphological characters alone appears not so promising (see Petersen, 1990), it is therefore preferable to wait with a revision until a thorough molecular analysis provides the necessary robust phylogeny. Meanwhile, the classification according to Bouillon (1985) is here used in order to maintain nomenclatural stability.

Through monotypy, the genus *Acauloides* Bouillon, 1965 is unfortunately based on *Acauloides ammisatum*, an insufficiently known species. *Acauloides* is thus essentially distinguished from *Acaulis* through the absence of filiform tentacles. The filiform tentacles of *Acaulis* are formed relatively late in development through the transformation of capitate tentacles (Berrill, 1952). Using this ontogenetic argument and also outgroup comparisons to the Tricyclusidae and Candelabridae, it is evident that filiform tentacles of *Acaulis* are apomorphic. The absence of filiform tentacles in the genus *Acauloides* is thus a plesiomorphic trait and unsuitable to reveal a monophyletic group. The genus *Acauloides* could nevertheless be valid, as in *Acauloides ilonae* the gonophores develop in the upper axils of the tentacles, which is clearly an apomorphy for this genus. Because *Acauloides ilonae* is perhaps a synonym of *A. ammisatum*, it is thus recommendable to continue to use the genus *Acauloides* in order to maintain nomenclatural stability.

#### KEY TO GENERA:

- 1a hydranth small, very elongated, all tentacles indistinctly capitate ..... *Cryptohydra* (not in European fauna)
- 1b majority of tentacles distinctly capitate ..... 2
- 2a mature hydranth with a whorl of thick filiform tentacles ..... *Acaulis*
- 2b all tentacles capitate ..... *Acauloides*



## Genus *Acaulis* Stimpson, 1854

TYPE SPECIES: *Acaulis primarius* Stimpson, 1854.

SYNONYMS: *Blastothela* Verrill, 1878: 374; ? *Myriocnida* Stechow, 1909 (invalid *nomen nudum*).

DIAGNOSIS: Hydroid connected to substrate by modified hydrocaulus secreting a gelatinous sheath or forming anchoring filaments; hydranth fusiform; capitate tentacles in one oral whorl and more scattered below, solid, with chordoid gastrodermis; below capitate tentacles one whorl of filiform, long, stout, aboral tentacles developing by transformation of capitate tentacles; gonophores fixed, carried singly or in clusters on short pedicels.

REMARKS: Stechow (1909) introduced the genus name *Myriocnida* for a hydroid described in Fewkes (1890) as *Acaulis* (without specific epithet). Because it was not based on a nominal species, the genus is not valid. It remains unclear to which species Fewkes' material belonged (he described it from notes made by someone else). It could have been either *Acaulis* or more likely an incomplete *Candelabrum* species.

## *Acaulis primarius* Stimpson, 1854

Fig. 1

*Acaulis primarius* Stimpson, 1854: 10, pl. 1 fig. 4; Allman, 1872: 378; Sars, 1874: 123, pl. 5 figs 14-20; Will, 1913: 57, pl. 26; Scheuring, 1922: 167, pl. 5 fig. 1; Berrill, 1952: 17, fig. 6; Rees, 1957: 466, fig. 13; Bouillon, 1971: 342, pl. 4; ? Verwoort, 1985: 269, plate 1; Schuchert, 2001a: 35, fig. 22A-D.

*Acaulis primaris* – Naumov, 1969: 243, fig. 112 [incorrect subsequent spelling].

MATERIAL EXAMINED: Material from Iceland and Greenland as given in Schuchert (2001a).

DIAGNOSIS: Acaulidae with filiform tentacles in mature animals, sporosacs not in axils of tentacles, base without attachment filaments.

DESCRIPTION: Solitary hydroids, body thickly fusiform to cylindrical, divided into basal part (approx. 1/5 of height, variable) and upper part. Both parts separated by one whorl of five to eight thick tapering tentacles covered evenly with nematocysts. Basal part conical to cylindrical, surrounded by thick jelly covered by adhering detritus. Upper part of hydranth roughly cylindrical with up to 50 scattered capitate tentacles; hypostome rounded. Gonophores on lower part of region with capitate tentacles but not associated with the tentacles. Gonophores sessile sporosacs with spadix but without radial or ring canals. Nematocysts: stenoteles, microbasic heteronemes (euryteles or mastigophores), and desmonemes.

DIMENSIONS: Mature polyps are 5 to 10 mm in height, extended up to 2 cm (Westblad, 1947), gonophores ca. 0.5-0.6 mm. Nematocysts: stenoteles, (18-21)x(14-17) mm; heteronemes, (16-20)x(7-10.5) mm; desmonemes, (12-15.5)x(8.5-10.5) mm.

DEVELOPMENT: Young hydranths have no filiform tentacles, only capitate ones. During growth, the lowest capitate tentacles become elongated and thicker, and the nematocyte free regions of the tentacles are subsequently covered by nematocytes (see Fig. 1A-B) (Berrill, 1952). The development of the gonophores can begin before the filiform tentacles have completed their transformation.



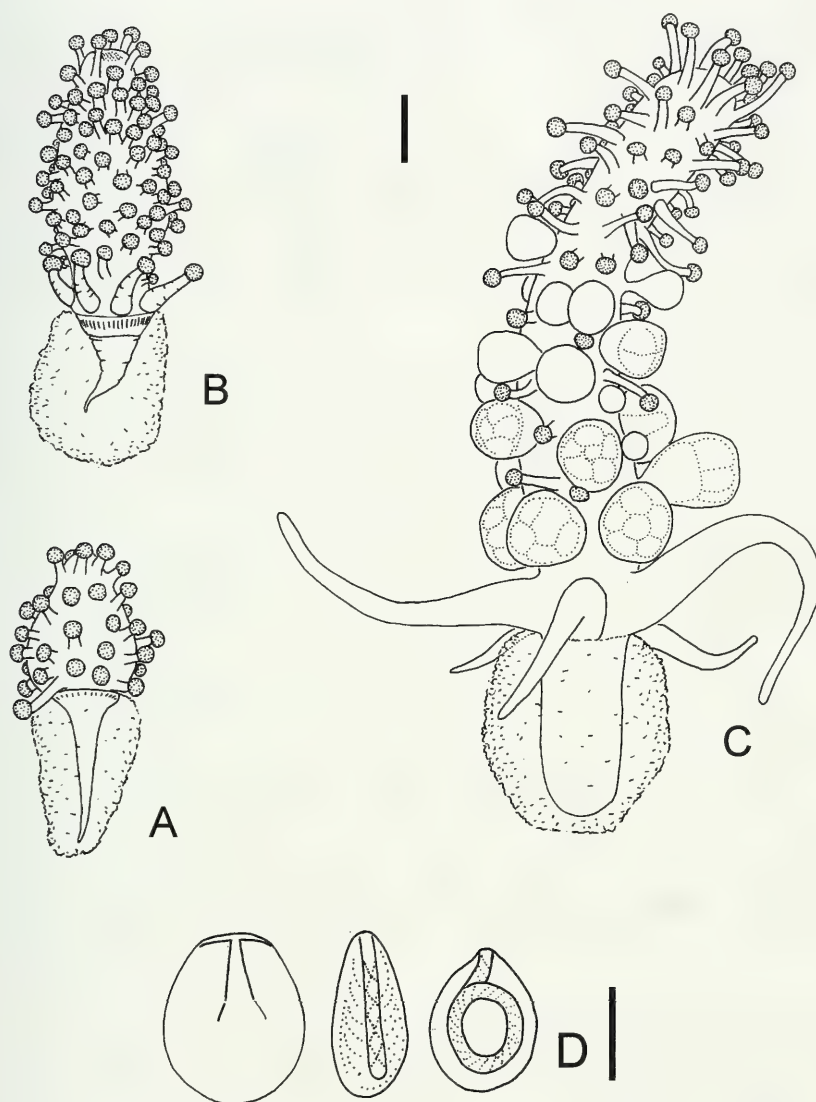


FIG. 1

*Acaulis primarius* Stimpson, 1854; after Schuchert (2001a), Icelandic material. A) Juvenile, scale bar 0.5 mm, also valid for sections B-C. B) Intermediate sized specimen with beginning transformation of lowest tentacles. C) Mature female, filiform tentacles fully developed. D) Nematocysts, as seen in preserved material: stenotele, microbasic heteroneme, desmoneme, scale bar 10  $\mu$ m.

ADDITIONAL DATA: Westblad (1947) describes and depicts both the gonophore development and gametogenesis. Westblad (1947) also depicts the nematocysts and describes their distribution.

**BIOLOGY:** *Acaulis primarius* lives usually partially embedded in sediment bottoms at depths of down to 350 m, usually not above 20 m depth (Berrill, 1952; Schuchert, 2001a).

**DISTRIBUTION:** Northern Atlantic, Arctic to boreal regions; New England, New Brunswick, north-west coast of Norway, Barents Sea, White Sea (Scheuring, 1922; Fraser, 1944; Naumov, 1969), North Sea, Sweden (Jäderholm, 1909; Westblad, 1937; Bouillon *et al.*, 1995), Baltic Sea (Will, 1913; Schönborn *et al.*, 1993), Iceland (Schuchert, 2001a), western Greenland (Schuchert, 2001a). Perhaps also Bay of Biscay (Vervoort, 1985, identification uncertain). Type locality: Grand Manan, Bay of Fundy, Canada.

**REMARKS:** Stimpson (1854) described *Acaulis primarius* based on two sets of animals collected at different times. The first animal he found and depicted corresponds exactly to our current concept of *Acaulis primarius*. The second set he found later, attached to red-algae (it is unclear in what depth, he states 5-15 f., which could be feet or fathoms, both interpretations can be found in the literature, but the latter being more probable). In the second set of specimens the tentacles were much longer, the hydranths resembled a corynid and they reportedly produced medusae. Allman (1872), Will (1913), and Fraser (1924) noticed this difference and assumed that the second set of Stimpson's material belonged to another species than *Acaulis primarius*. Allman (1872) restricted the scope of *Acaulis* to the animal depicted in Stimpson (1854), thus he *de facto* selected a lectotype and *Acaulis primarius* is thus well defined.

### Genus *Acauloides* Bouillon, 1965

TYPE SPECIES: *Acauloides ammisatum* Bouillon, 1965, by monotypy.

SYNONYMS: ? *Psammocoryne* Monniot, 1962 (invalid *nomen nudum*).

**DIAGNOSIS:** Hydroid attached to substrate by modified hydrocaulus, secreting a gelatinous sheath or mucous film; capitate tentacles in one oral whorl and more scattered below, solid, with chordoid gastrodermis; without filiform tentacles; gonophores in upper axils of tentacles, asexual reproduction through transverse fission.

### *Acauloides ammisatum* Bouillon, 1965

Fig. 2

? *Psammocoryne*. – Monniot, 1962: 274, fig. 14b [*nomen nudum*].

*Acauloides ammisatum* Bouillon, 1965: 54; Bouillon, 1971: 335, figs IV8-11, V-VI; Bouillon *et al.*, 2004: 86, fig. 47H.

**MATERIAL EXAMINED:** None, type material could not be located.

**DIAGNOSIS:** Acaulidae with capitate tentacles only, adults 0.6-2 mm, 10-25 tentacles, peduncle without gelatinous tube, only mucous secretion at its end for attachment to sand grains.

**DESCRIPTION:** Solitary hydroids, thick fusiform shape, short peduncle of about 1/3 of total height, peduncle without gelatinous tube but at end mucous secretion by which the animal attaches itself to sand grains. Tentacles all capitate, 10-25, one oral whorl of 4-6 short tentacles, remaining scattered below on body, those in middle of body longest, others very short to almost lacking a stalk. Nematocysts: stenoteles;

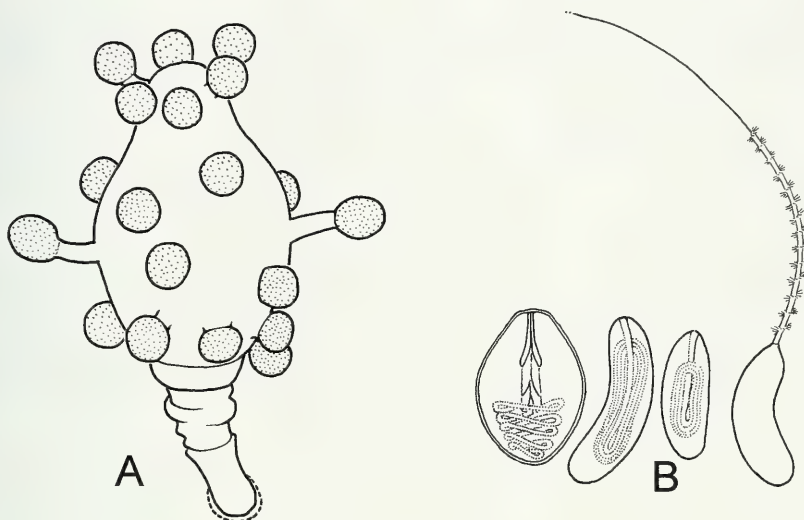


FIG. 2

*Acauloides ammisatum* Bouillon, 1965; modified after Bouillon (1971), no scale given. A) Polyp. B) Stenotele, larger mastigophore, smaller mastigophore, discharged mastigophore.

desmonemes; holotrichous microbasic mastigophores, when discharged shaft longer than capsule. Vegetative and sexual reproduction not known.

**DIMENSIONS:** Polyps 0.6-2 mm. Nematocysts: stenoteles  $17 \times 14 \mu\text{m}$ , desmonemes  $6 \times 10 \mu\text{m}$ , microbasic mastigophores  $(16-18) \times (6-8) \mu\text{m}$ .

**ADDITIONAL DATA:** Bouillon (1971) provides further details on the histology and cytology of this species.

**DISTRIBUTION:** Roscoff, Brittany; ? Banyuls-sur-Mer (Mediterranean). Type locality: Roscoff, English Channel.

**REMARKS:** *Acauloides ammisatum* Bouillon, 1965 strongly resembles the vegetative reproduction stage of *A. ilonae* (Brinckmann-Voss, 1966) and the two are possibly conspecific. There are some minor size differences, with *A. ammisatum* being smaller and having slightly larger nematocysts. Another formal difference is the absence of a gelatinous tube in *A. ammisatum*, for which only a mucous cover has been described. However, such a mucus cover might be only the initial stage of a gelatinous tube, a type of cover which is only seen in fully grown animals. There is also a possible ecological difference: while *A. ammisatum* occurs on sand, *A. ilonae* has been found on mud only. More data – especially on mature animals from Roscoff – are needed before a final more definite conclusion is possible. Meanwhile, both nominal species should be kept separate.

Bouillon (1971) also attributed to this species some animals from Banyuls (Mediterranean) depicted in Monniot (1962). Monniot found her animal in coarse sand and identified it as *Psammocoryne*. This name is not a valid genus as it was not asso-

ciated with a valid nominal species. Furthermore, Monniot's hydroid could easily also be referred to *A. ilonae* and it is therefore also somewhat unclear whether *A. ammisatum* also occurs in the Mediterranean (this in case that they are not conspecific).

***Acauloides ilonae* (Brinckmann-Voss, 1966)**

Fig. 3

*Acaulis ilonae* Brinckmann-Voss, 1966: 292, figs 1-10; Brinckmann-Voss, 1970: 44, text-fig. 51, pl. 1 figs 4-6.

*Acauloides ilonae* – Bouillon *et al.*, 2004: 86, fig. 471.

MATERIAL EXAMINED: Syntypes (labelled holotype), BMNH 1963.12.9.1, as *Acaulis ilonae*, two specimens, both broken. – BMNH 1974.11.21, as *Acaulis ilonae*, Naples, 20.10.1960-29.11.1961, leg. Brinckmann-Voss, one female, pedicel broken off.

DIAGNOSIS: Acaulidae with capitate tentacles only, sexually reproducing adults 5-10 mm, about 2 mm in phase of vegetative reproduction; sporosacs in upper axils of tentacles, peduncle of adult hydranths in gelatinous sheath.

DESCRIPTION (after Brinckmann-Voss, 1966; 1970; and own observations): Mature hydroid spindle shaped, divided into two parts of roughly the same length: an upper tentacle-bearing part and a basal part without tentacles called peduncle (or "foot"). Peduncle tapering, surrounded by a gelatinous sheath which adheres to mud particles or cultivation vessels, gastrodermis highly vacuolated. Tentacles all capitate, solid, up to 60, one oral whorl of four to five tentacles and a basal whorl comprising the same number of tentacles, between them a number of scattered tentacles, often in groups of two to three around a sporosac, tentacle length unequal, longest ones more proximal, diameter of capitula also variable. Gonophores are sporosacs without radial canals, developing always in upper axils of tentacles in middle region of tentaculate part, oldest sporosacs in middle, younger ones proximal and distal to them. New tentacles often formed close to the gonophores. Colour of the animals pink to orange, with a number of white dots on surface, very old specimens have a brownish colour, nematocysts: stenoteles, microbasic euryteles and desmonemes. Fertilized eggs developing a capsule and going through an encysted resting stage.

Polyps in vegetative phase of reproduction small, with 29-35 tentacles, attached to substratum, multiplying by binary fission in region of tentacles.

DIMENSIONS: Sexually reproducing animals up to 10 mm, polyps in phase of vegetative multiplication up to 2 mm. Diameter of eggs 0.15 mm. Nematocysts: desmonemes (8.4-12.6)x(7.6-9.2) $\mu$ m; stenoteles (18.5-22.7)x(16.0-19.3) $\mu$ m; microbasic euryteles (11.8-14.3)x(3.4-7.6) $\mu$ m (Brinckmann-Voss, 1966).

DISTRIBUTION: Naples, questionably also Roscoff, Brittany, although the latter records may refer to *A. ammisatum*. Type locality: Gulf of Pozzuoli, Naples, Italy, 45 m.

BIOLOGY (after Brinckmann-Voss, 1966; 1970): *Acauloides ilonae* is able to creep sluggishly on the substrate. The animals are gonochoristic; female and male hydroids continue to spawn their gametes several times for more than a year, the gametes differentiate continuously. Eggs are usually shed during the night and early morning hours, fertilisation takes place in the seawater. The embryo does not swim and attaches itself to the ground and transforms into a flattened body which is covered with thin, transparent cuticula. The cyst remains attached for at least one month, after which a



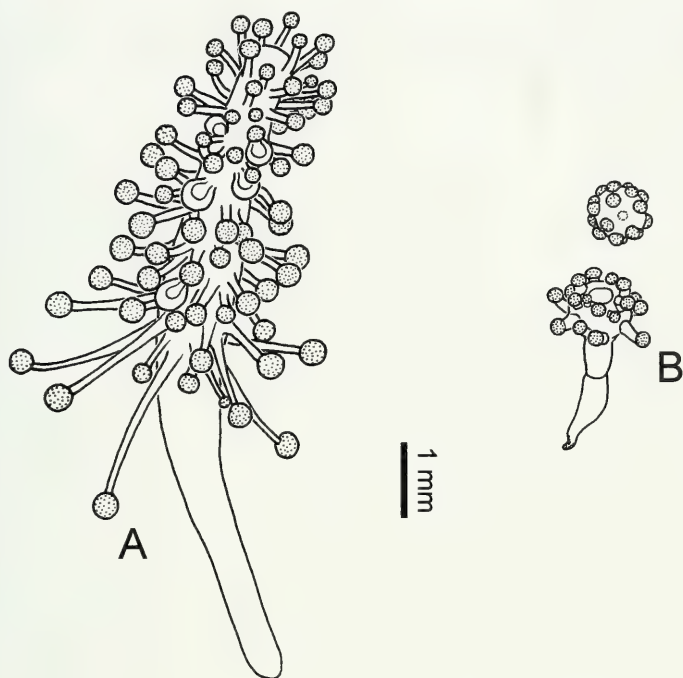


FIG. 3

*Acauloides ilonae* (Brinckmann-Voss, 1966), modified after Brinckmann-Voss (1966), scale bar 1 mm. A) Sexually reproducing polyp. B) Vegetatively reproducing polyp just after fission, with aboral and oral parts.

small polyp without tentacles hatches very slowly (it takes 2-3 days). Hydroids hatch from cysts only if kept in water of 13°C, at 20°C the hatching rate is poor. The young polyp grows to a size of about 2 mm and then starts the vegetative reproduction phase by transverse fission. At 20°C divisions take place every 10-45 days and if kept at 20° the fission continues, the polyps do not exceed 2-3 mm, and they do not develop gonophores. Polyps that had undergone divisions and are brought to 13° do not divide anymore, they begin to grow in length, get more tentacles and develop gonophores in the axils of the tentacles, thus starting the sexual phase. Individuals that had hatched from cysts and are cultured at 13° undergo one or two rounds of divisions before they develop gonophores. Sexual maturity is not reached without having first undergone asexual division.

The hydroid was found on surface of mud in depths of 20 to 80 m. It occurred in abundance around Naples from November to April. It was not found from July to October. It is thus a winter species.

REMARKS: Brinckmann-Voss (1966) described her material based on animals from Naples, but also mentioned that Bertil Swedmark had found it at Roscoff too (via personal communication by J. Rees). Because it appears that the latter material was

more likely *Acauloides ammisatum* (see remarks in Bouillon, 1971: 335), the occurrence of *A. ilonae* outside the Mediterranean is uncertain (if the two indeed prove to be distinct species, see remarks under *A. ammisatum*).

#### FAMILY BOREOHYDRIDAE WESTBLAD, 1947

TYPE GENUS: *Boreohydra* Westblad, 1937.

DIAGNOSIS: Hydroids solitary, small, with one whorl of reduced tentacles, capitate or not, located in the oral or median part of body; perisarc covering of base filmy or absent; gametes in body wall.

REMARKS: Representing likely a simplified form, the affinities of the genus *Boreohydra* with its sole species *B. simplex* remains controversial. Westblad (1947) considered it related to the Tubulariidae, but sufficiently distinct to deserve being placed in a separate family. Rees (1957) could not agree and placed it in the Corymorphidae. Calder (1974) thought that if the nematocyst clusters on the body should prove to be nothing but reduced capitate tentacles, then the genus should belong to the Candelabridae. Bouillon (1985) considered the family Boreohydridae as valid and added also the genus *Psammohydra* to it, this because of the resemblance of their cnidome. Petersen (1990) placed *Boreohydra* among the Acaulidae, but gives no arguments for this and he does not discuss *Psammohydra*. As already stated for the family Acaulidae, the problem is not resolvable by traditional approaches and, pending a molecular analysis, the family *Boreohydridae* is here retained for the time being.

#### KEY TO THE GENERA:

- 1a     hydranth with oral capitate tentacles and nematocyst buttons on body . . . . . *Boreohydra*
- 1b     filiform tentacles in middle of body; hypostome proboscis-like . . . . . *Psammohydra*

#### Genus *Boreohydra* Westblad, 1937

TYPE SPECIES: *Boreohydra simplex* Westblad, 1937.

DIAGNOSIS: Solitary hydroids of small size, living buried in the sediment; caulus covered by filmy perisarc; one whorl of capitate tentacles near mouth and numerous scattered nematocyst clusters on hydranth body. Gametes in epidermis at junction of hydranth body and caulus; asexual reproduction by transverse fission.

REMARKS: This is currently a monotypic genus.

#### *Boreohydra simplex* Westblad, 1937

Fig. 4

*Boreohydra simplex* Westblad, 1937: 1, figs 1-4; Westblad, 1947: 1-13, figs 1-4, pls 1-3; Nyholm, 1951b: 531, text fig., pl. 1 figs 1-4; Westblad, 1953: 351, figs 1-2; Prévot, 1959: 97, pl. 1 fig. 2; Calder, 1974: 1666, fig. 1; Bozhenova *et al.*, 1989: 11, fig.; Petersen, 1990: 148; Schuchert, 2001a: 36, fig. 23A-B; Bouillon *et al.*, 2004: 86, fig. 47L.

MATERIAL EXAMINED: See Schuchert (2001a).

DIAGNOSIS: Small, solitary, mud-dwelling hydroids with three to four capitate oral tentacles and scattered wart-like nematocyst clusters on hydranth body.

DESCRIPTION: Solitary hydroid, composed of hydranth body and conical peduncle. Hydranth spindle-shaped, hypostome short and rounded, surrounded by



FIG. 4

*Boreohydra simplex* Westblad, 1937; Northern Greenland, Pearyland, after Schuchert (2001a). A) polyp, scale bar 0.2 mm. B) stenotele, desmoneme, isorhiza, scale bar 10  $\mu$ m

three to four short, stubby tentacles, only slightly capitate. On hydranth body 50-60 scattered nematocyst clusters, variable in size, 3-15 capsules per cluster, clusters slightly elevated and wart-like. Hydranth body at base tapering and turning into peduncle, peduncle conical, constantly tapering into fine tip at its end, covered by wrinkled perisarc. Gastrodermis with three or four longitudinal folds. Nematocysts: stenoteles; desmonemes, discharged with four coils; isorhizas.

**DIMENSIONS:** Hydranth body height 0.8-1.5 mm, diameter about 0.3 mm; peduncle 0.4-1 mm long. Nematocysts: stenoteles (17-19)x(16) $\mu$ m; desmonemes, (16-17)x(9-11) $\mu$ m; isorhizas (17-20)x(4.5-5.5) $\mu$ m.

**BIOLOGY:** Fairly common in mud bottoms characterized by the '*Brissopsis lyrifera* - *Amphiura chiajei*' community (Petersen, 1913; Jones, 1950) at depths of around 40 m (Westblad, 1953). The depth range varies from a few metres to more than 600 m (Christiansen, 1972). The animal is able to move quite rapidly on the surface of mud (Hult, 1941). The latter author also described how it burrows into the mud. The oral tentacles are instrumental for this process. The food seems to be mainly composed of small nematodes (Westblad, 1947).

**ADDITIONAL DATA:** (Westblad, 1947; Nyholm, 1951b) The polyp multiplies by transverse fission and produces gonophore-like outgrowths without germ-cells. Eggs were found in the epidermis at the junction of the body and peduncle. Westblad (1947) gives further details on the variability: of 60 animals, 47 had three tentacles, the others four. The number of tentacles and the number of gastrodermal folds is not closely correlated. Prévot (1959) depicts a longitudinal section. Bozhenova *et al.*, (1989) depict the nematocysts and provide measurements.

**DISTRIBUTION:** Bipolar, northern and southern Atlantic Ocean in temperate to Arctic waters, probably quite frequent, but often overlooked. It was particularly often recorded along the Atlantic coast of Scandinavia. The southern limit for Europe is the English Channel. Recorded from the White Sea, Norway to Sweden, Great Britain, Iceland, North Greenland, North-Eastern Canada, North Greenland, South Georgia (Hult, 1941; Westblad, 1953; Christiansen, 1972; Calder, 1974; Bozhenova *et al.*, 1989; Schuchert, 2001a). Type locality: Tromsø and Ramfjord, Norway.

**REMARKS:** Westblad (1947) supplemented the first description by further anatomical and ecological details. He observed buds that he interpreted as gonophores, however he could not find germ cells in them. Later, Nyholm (1951) observed eggs in the epidermis and concluded that the germ cells of this species are not collected in sporosacs, but remain in the epidermis like in *Hydra*. Petersen (1990) interpreted the gonophore-like outgrowths observed by Westblad (1947) as incipient polyp buds. More work is needed to reveal the nature of these buds.

#### Genus *Psammohydra* Schulz, 1950b

**TYPE SPECIES:** *Psammohydra nana* Schulz, 1950b.

**DIAGNOSIS:** Solitary hydroids of very small size, living attached to sand grains; one whorl of filiform tentacles in middle region of hydranth; hypostome proboscis-like, with terminal swelling. Asexual reproduction through fission.

**REMARKS:** This is currently a monotypic genus. The sexual reproduction is insufficiently known.

#### *Psammohydra nanna* Schulz, 1950

Fig. 5

*Psammohydra nanna* Schulz, 1950b: 122, figs 1-9; Riedl, 1970: 153, pl. 43; Clausen, 1971: 2, fig. 1; Clausen & von Salvini-Plawen, 1986: 34, fig. 3; Thiel, 1988: 267, fig. 19.1d; Bouillon *et al.*, 2004: 87, fig. 48A.

**MATERIAL EXAMINED:** None, the type material could not be located.

**DIAGNOSIS:** Very small solitary hydroid living attached to sand grains, body skittle- to spindle shaped, one whorl of filiform tentacles in about middle of body.

**DESCRIPTION:** Tiny solitary hydroids, living attached to sand-grains; body shape and size very variable, usually skittle- or spindle-shaped, with flat base when attached, slightly above middle a single whorl of four (rarely 3-5) tentacles; hydranth body above tentacles proboscis-like, with terminal swelling. Proboscis movable and extensible, mouth terminal but invisible when not used. Tentacles short, straight, contractile, filiform, nematocysts evenly distributed, gastrodermis chordoid. Sexual reproduction insufficiently known, reportedly only one egg is produced. Colour: sand-grey. Nematocysts: stenoteles, desmonemes, atrichous isorhizas.

**DIMENSIONS:** Total body size 0.28-0.4 mm, but very variable, can contract or expand its body about two times. Nematocysts: stenoteles (6-7)x(5-6) $\mu$ m, isorhizas (5.5-6.8)x(2.3-3) $\mu$ m; desmonemes (3.5-5.5)x(2.3-3.5) $\mu$ m (Schulz, 1950b).

**BIOLOGY:** Vegetative reproduction takes place by transverse fission. The animal can move by creeping like a freshwater *Hydra*. It is a member of the meiofauna and



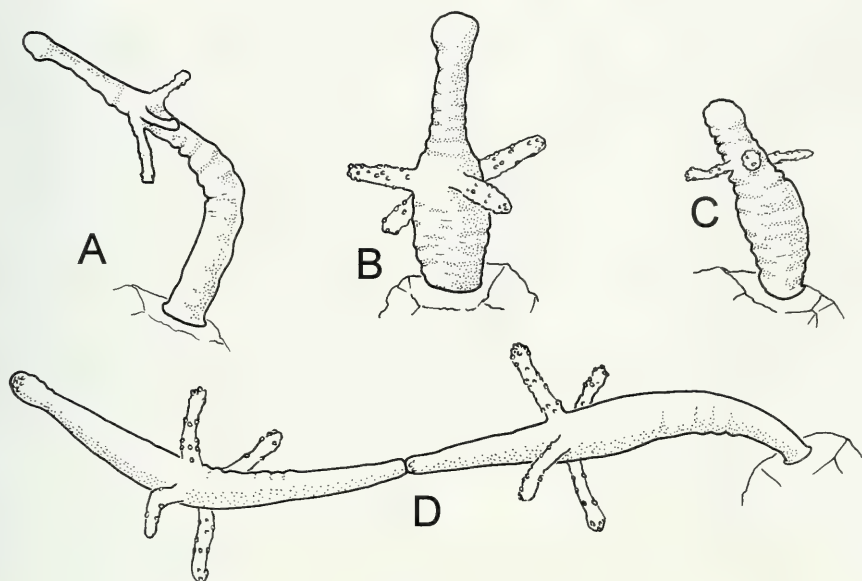


FIG. 5

*Psammohydra nanna* Schulz, 1950, redrawn from Schulz (1950b), no scale given. A-C) Animals on sand-grains in various states of contraction. D) Vegetative reproduction by transverse fission.

occurs in fine sand in shallow waters of a few metres. Schulz (1950b) characterizes the community where it was found as "*Turbanella hyalina*" community (Remane, 1933). It can tolerate reduced salinity down to 8‰ (Schönborn *et al.*, 1993).

**ADDITIONAL DATA:** Of 46 examined animals, 39 had four tentacles, four had three tentacles, and three five (Schulz, 1950b). Schulz (1950b) also describes the histology of this animal. The gastrodermal epithelium is high in the lower part of the animals, almost obliterating the lumen, but it is low above the tentacles and thus leaves a distinct cavity. The proboscis contains only stenoteles and isorhizas. The desmonemes are confined to the tentacles. The proboscis is very extensible and can bend to all sides. It acts like a central tentacle and it is used for locomotion and food capture. Swedmark (1959) mentions without further comment that *Psammohydra* produces a single egg only.

**DISTRIBUTION:** Western Baltic Sea (Schulz, 1950b), English Channel (Teissier, 1965); western Mediterranean (Swedmark, 1956), Adriatic Sea (Salvini Plawen, 1966).

**REMARKS:** The taxonomic position of this simplified animal is unclear (see also remarks for family Acaulidae and Boreohydridae).

**FAMILY PROTOHYDRIDAE** Allman, 1888

**TYPE GENUS:** *Protohydra* Greeff, 1869.

**DIAGNOSIS:** Solitary, small, elongated hydroids usually living in brackish-waters; without tentacles and gonophores, pedal disc formed by epidermal cells only;

gametes bulging into gastric cavity, nematocysts: stenoteles and isorhizas, evenly distributed over body.

Genus *Protohydra* Greeff, 1869

TYPE SPECIES: *Protohydra leuckarti* Greeff, 1869.

DIAGNOSIS: With the characters of the family.

REMARKS: Due to their – likely secondary – very simple morphology, the Protohydrae are difficult to classify. Petersen (1990) treated the family as *Capitata incerta sedis*. The cnidome is quite interesting as it lacks desmonemes. This could, however be due to the absence of tentacles. In *Psammohydra nanna*, a similarly reduced form, the desmonemes are associated with the tentacles. The family currently comprises two species: *Protohydra leuckarti* Greeff, 1869 and *Protohydra psamathe* Omer-Cooper, 1964. *Protohydra caulleryi* Dawydoff, 1930, characterized by budding or frustules, is likely a polyp belonging to the Oliandiasidae (Weill, 1935; Schulz, 1952).

*Protohydra leuckarti* Greeff, 1869

Fig. 6

*Protohydra leuckarti* Greeff, 1869: 37, pls 4-5; Luther, 1923: 1, figs 1-11; Koller, 1927: 97, figs 1-2; Westblad, 1930a: 1-4; Westblad, 1930b: 1-13, figs 1-3; Weill, 1934: 448; Weill, 1935: 83, fig. 5; Westblad, 1935: 152, figs 1-4; Vervoort, 1946: 47, fig. 1; Schulz, 1950a: 53; Nyholm, 1951a: 529, pl. 1; Naumov, 1969: 593, fig. 439; Clausen, 1971: 1.

MATERIAL EXAMINED: ZMUV, Denmark, Mariagerfjord, Ajstrupbugt, 0.5 m, 31 July 1955, 3 specimens, det. Kramp. – IRSN, two samples from Roscoff, collected by J. Bouillon in May 1964 (many specimens) and August 1961 (few specimens).

DIAGNOSIS: Solitary, small, elongated hydroids without tentacles and gonophores, gametes bulging into gastric cavity; vegetative reproduction usually by transverse fission or rarely by lateral buds; nematocysts: stenoteles and isorhizas.

DESCRIPTION: Solitary, brackish-water hydroids, usually elongate spindle- to club-shaped when relaxed, spherical when contracted. Tentacles absent, at aboral end a small epidermal attachment disc for temporary attachment, no perisarc, nematocysts evenly distributed in epidermis, not concentrated around mouth. Vegetative reproduction by transverse fission, rarely by buds (Schulz, 1952). Gonophores absent, gametes differentiate from epidermal cells and proliferate into gastric cavity where the gonad remains attached along one side of the body wall, gonochoristic, females produce one egg only which is expelled by perforation of the body wall. Nematocysts (Luther, 1923; Weill, 1934; Schulz, 1950b): stenoteles and basitrichous isorhizas, desmonemes absent.

DIMENSIONS: Adults maximally contracted to a sphere 0.4 mm, expanded 2-3 mm (Greeff, 1869). Eggs ca. 0.25 x 0.14 mm (Westblad, 1930b). Nematocysts (Luther, 1923): stenoteles 12-17 µm long, isorhizas (7)x(3-3.5)µm,

ADDITIONAL DATA: There are pigment granules of variable size in the gastrodermis. The colour of the animals depends on the food items and is either colourless or various shades of red (Greeff, 1869; Madsen, 1939). Westblad (1935) showed that the germ cells originate from epidermal cells that proliferate into the gastric cavity. The animals are gonochoristic and females produce a single egg. The egg is expelled by a

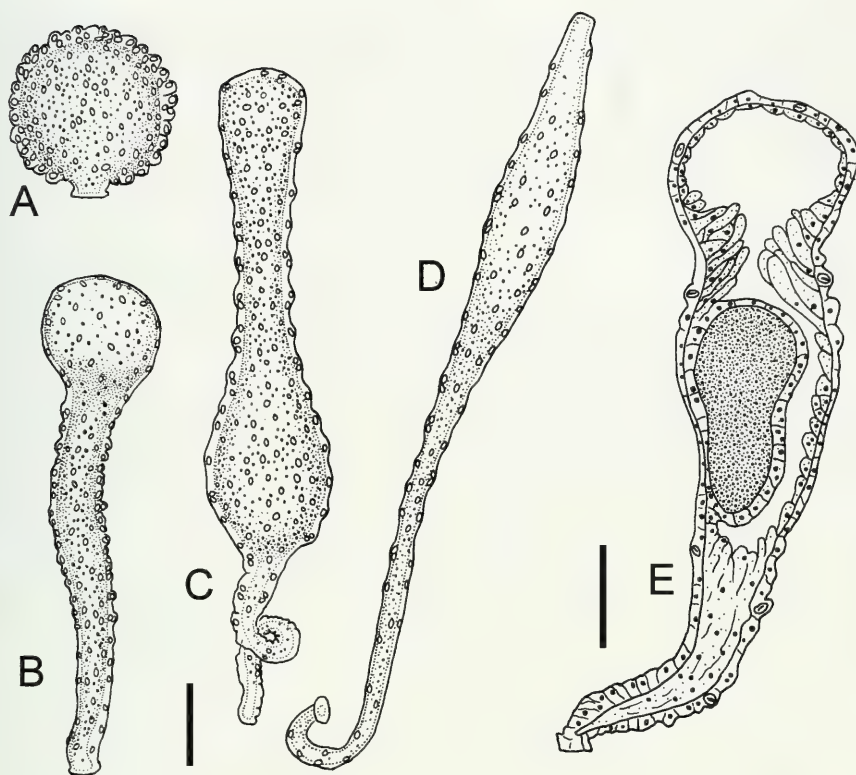


FIG. 6

*Protohydra leuckarti* Greeff, 1869. A-D) Animal in various states of contraction, oral end upwards, scale bar approximately 0.2 mm, redrawn from Greeff (1869). E) Schematic longitudinal section of male animal, the gonads (stippled) bulge into the stomach lumen, scale bar 0.1 mm, redrawn from Westblad (1935).

rupture of the body wall and the animal dies afterwards. Westblad (1935) also made some observations that hint at a possible copulation. This is rather exceptional for hydrozoans and needs reconfirmation. Schulz (1952) observed that besides the usual transverse fission, rarely some animals produce lateral polyp buds. Further biological data are also provided by Muus (1966) and Wehling (1978). Some information on the histology – e. g. the body wall, the glue cells, and gametogenesis – are provided by Luther (1923) and Westblad (1935).

**BIOLOGY:** A coastal, euryhaline species occurring in brackish waters of wave protected habitats, often in closed bays, estuaries, and lagoons. It is absent from agitated waters. The depth range is from a few cm to about 20 m and the reported salinity range 0.38–30‰ (Westblad, 1930a; Madsen, 1939; Schulz, 1950a; Schönborn *et al.*, 1993, Barnes, 1994). Various bottom types have been reported, but there seems to be a preference for fine sand or mud with much detritus. They can reach very high densities, reaching from 1000 individuals per square metre in winter to 50'000 in



summer, or even exceptionally 200'000/m<sup>2</sup> (Heip, 1971). Rarely it also occurs on algae. It can be found all year round, but reaches maximum densities in summer when it also gets sexually mature. *Protohydra leuckarti* is an important predator in its biotope and it regulates the density of other animals (Heip, 1971; Heip & Smol, 1976). The animal is able to creep and to burrow. It lives on a variety of food items, especially nematodes, copepods, ostracods, chironomid larvae (Schulz, 1950a). It is preyed upon by e. g. nudibranchs (Evertsen *et al.*, 2004).

**DISTRIBUTION:** Circumglobal in temperate brackish waters of the northern hemisphere. The northern limit in Europe is southern Norway (Oslofjord: Christiansen, 1972) and southern Finland (Helsinki: Schneider, 1927). It has been reported from the Atlantic coast of Sweden (Westblad, 1930a); the Baltic Sea (Schneider, 1927; Westblad, 1935; Koller, 1927; Nyholm, 1951; Schulz, 1950a); Denmark (Madsen, 1939; Muus, 1966; Rasmussen, 1973); German part of the North Sea (Schulz, 1950a); Holland (Boaden, 1976); Belgium (Greeff, 1869; Heip, 1971); Southern England (Baker, 1913; Hickson, 1920); Brittany (Teissier, 1965); Bay of Biscay (Nyholm, 1951a); in the Mediterranean it was found in brackish water lakes of southern France (Nyholm, 1951a). It has also been found in the Black Sea (Valkanov, 1947; Marcoci, 1956). Outside Europe it has been recorded on the east coast of North America (Ruebush, 1939), in the north-eastern Pacific (Wieser, 1958), the north-western Pacific (Naumov, 1969), and the Aral Sea (Maier, 1974). Type locality: Ostende, in mud among oyster cultures.

#### **FAMILY CANDELABRIDAE STECHOW, 1921**

**TYPE GENUS:** *Candelabrum* de Blainville, 1830: 284.

**SYNONYMS:** Myriotheidae Hincks, 1868; Symplectaneidae Fraser, 1941.

**DIAGNOSIS:** Large, worm-like hydroids, solitary or forming small pseudo-colonies through connected aggregates, attached to substrate but without stolons; hydranth elongated, cylindrical to club-shaped; with numerous scattered, hollow or parenchymatic capitate tentacles, tentacles simple or compound, if compound then with adnate basal parts. Hydrocaulus with or without perisarc, with tentacle- or root-like attachment-processes. Gonophores fixed sporosacs, developing either directly on hydranth body or on club-shaped blastostyles.

**REMARKS:** Stechow (1921: 248) pointed out that the genus *Candelabrum* de Blainville, 1830 has priority over *Myriothea* Sars, 1850. Consequently, he then also changed the family name from Myriotheidae Hincks, 1868 to Candelabridae Stechow, 1921. According to the ICZN [4<sup>th</sup> ed. 1999, 40.2] such a name change is valid if it was made before 1961 and if the new name has been widely used. The name Candelabridae has only recently come into usage (e. g. Bouillon, 1985; Schuchert, 1996; Hewitt & Goddard, 2001), while other used Myriotheidae (e. g. Calder, 1972; Millard, 1975; Petersen, 1990). I therefore suggest that for the sake of nomenclatural stability, Candelabridae should be used from now on. This name matches the genus name and it is also used in several large electronic databases. If in future Candelabridae should not become the prevailing name, then a ruling of the International Commission on Zoological Nomenclature must be requested.



The family currently comprises the following genera: *Candelabrum* de Blainville, 1830; *Monocoryne* Broch, 1910, and *Fabulosus* Stepanjants, 1990.

KEY TO THE GENERA:

- 1a capitate tentacles simple ..... 2
- 1b capitate tentacles compound ..... *Monocoryne*
- 2a sporosacs borne on blastostyles ..... *Candelabrum*
- 2b sporosacs borne singly on hydranth body ..... *Fabulosus* (not in European fauna)

Genus *Candelabrum* de Blainville, 1830

TYPE SPECIES: *Lucernaria phrygia* Fabricius, 1780 = *C. phrygium* (Fabricius, 1780).

SYNONYMS (after Segonzac & Vervoort, 1995): *Arum* Vigurs, 1850; *Myriothele* M. Sars, 1850; *Spadix* Gosse, 1853a; *Acandela* Stechow, 1920.

DIAGNOSIS: Solitary hydroids or loose aggregates comprising few polyps that may have a common perisarc base. Hydranth long, cylindrical or club-shaped, upper part with numerous simple capitate tentacles; at base a foot region, with or without perisarc sheath, with attachment processes that are either covered with perisarc or naked and may have a perisarc disc at their end; gonophores are fixed sporosacs borne on blastostyles developing in region between tentacles and foot. With or without clasper tentacles that hold developing embryos. Development direct, leading to young polyps without a planula stage.

REMARKS: Segonzac & Vervoort (1995) recently revised the genus *Candelabrum*, outlining its synonymy and taxonomic history.

KEY TO THE NORTH-ATLANTIC *CANDELABRUM* SPECIES:

- 1a sporosacs without nematocyst buttons ..... 2
- 1b sporosacs with nematocyst buttons ..... *C. verrucosum*
- 2a foot large, covered by perisarc sheath, hermaphroditic ..... 3
- 2b foot without perisarc sheath, without clasper tentacles, dioecious, deep water or Arctic form ..... *C. phrygium*
- 3a boreal shallow water form, with clasper tentacles holding developing embryos ..... *C. cocksii*
- 3b deep water form, without clasper tentacles ..... *C. serpentarii* (not in European fauna)

*Candelabrum cocksii* (Cocks, 1854)

Fig. 7

*Arum Cocksii* Vigurs, 1850: 90, *nomen nudum*.

*Spadix purpurea* Gosse, 1853a: 126; Cocks, 1853: 365.

*Spadix cocksii* – Gosse, 1853c: 386.

*Arum cocksii* Cocks, 1854: 34, pl. 3, fig. 7-12.

*Myriothele phrygia* – Hincks, 1868: 77, pl. 12 fig. 3; Allman, 1874: 317; Hardy, 1891: 505, pls 36-37; Hartlaub, 1916: 110, figs 38-39.

[not *Candelabrum phrygium* (Fabricius, 1780)]

*Myriothele* – Allman, 1876: 549, pls 55-58 [only named *Myriothele phrygia* in plates].

*Arum cocksii* – Rees, 1957: 487, figs 37 & 39A-B; Prévot, 1959: 97, pl. 1 fig. 1.

*Myriothele cocksii* – G. O. Sars, 1874: 130; Bonnevie, 1899: 36; Billard, 1921: 12, fig. 1; Weill, 1934: 373; Manton, 1941: 143, figs 1a-b, 2.

*Candelabrum cocksii* – Segonzac & Vervoort, 1995: 37, fig. 2c-d, table 1.

MATERIAL EXAMINED: MHNG INVE 36299, France, Roscoff, near Ile Verte, 0 m, 17 September 2004, 3 specimens, fertile, examined alive, one blastostyle used for serial histological sections, confirming the presence of two male sporosacs and several female ones. – MHNG INVE 29591, France, Roscoff, near Île Verte, 0 m, 30 March 1998, 2 specimens,

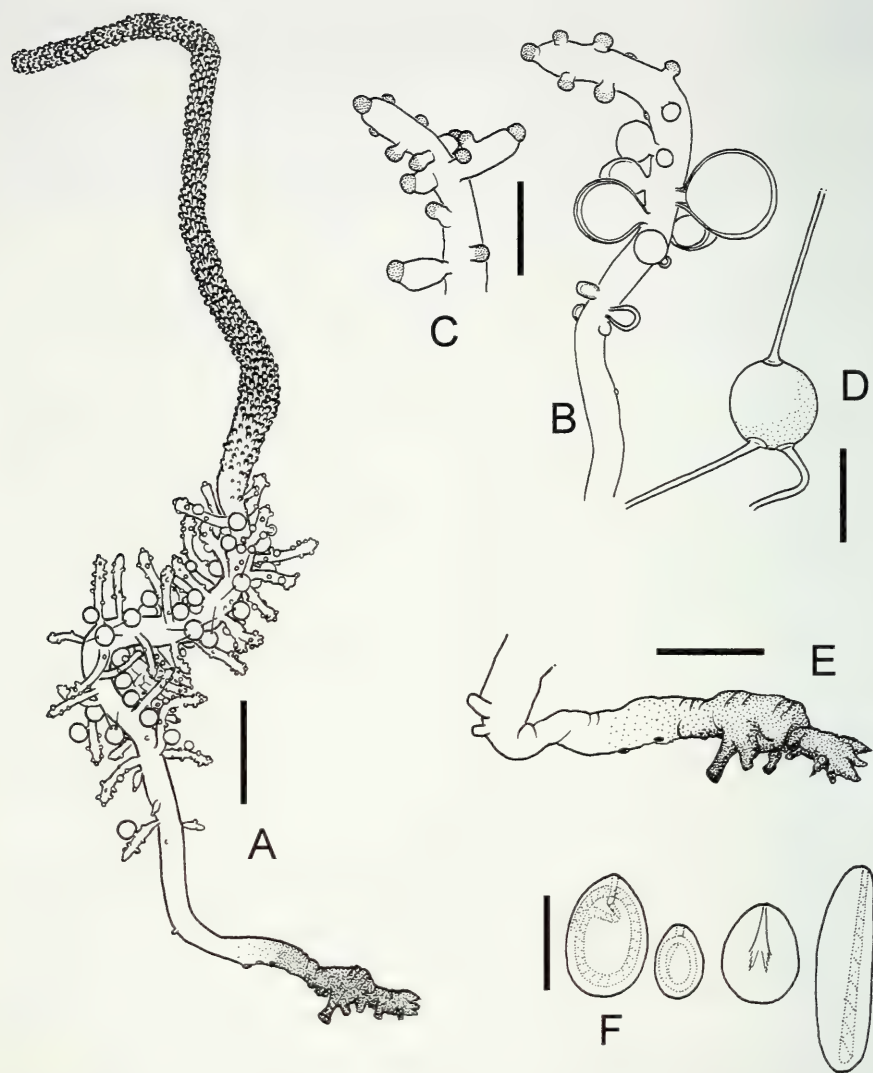


FIG. 7

*Candelabrum cocksii* (Cocks, 1854); A, after photographs of living animals, C-F, after preserved material. A) Entire polyp, semi-extended, capitate tentacles contracted, scale bar approximately 5 mm. B) Blastostyle with sporosacs and capitula (stippled), scale bar 1 mm. C) Tip of blastostyle with branched end, same scale as B. D) Embryo held by three clasper tentacles, scale bar 1 mm. E) Attached base of hydranth, perisarc dark, note two small perisarc discs in lighter region, scale bar 3 mm. F) Nematocysts of mature polyp: large and small desmonemes, stenotele, microbasic eurytele, scale bar 10  $\mu$ m.

attachment part lacking, fertile, 28S sequence of this material in GenBank under accession number AY920796, 18S AY920758, 16S AY787879. – MHNG INVE 35726, France, Roscoff, Tyaozon, 6 May 1910, coll. M. Bedot. – BMNH 1980.3.1.1, misidentified as *Candelabrum phrygium*, England, Devon, Salcombe, Castle Rock, 19 Feb 1980, R. L. Manuel, 3 well preserved specimens, eggs held by claspers present, base in irregular perisarc.

**DIAGNOSIS:** *Candelabrum* species with clasper tentacles that hold embryos, hermaphroditic, base long and sheathed in perisarc envelope that is adnately attached to the substratum.

**DESCRIPTION:** Solitary, relatively large, firmly attached, worm-like polyps, divided into three regions: foot, blastostyle region in middle, and trunk.

Foot large, about 1/4 to 1/3 of whole animal, bent horizontally so that attachment to substrate is adnate, basal region encased in firm, brown perisarc, distorted and gnarled to fit irregularities of the substratum and provided with short, lobed or finger-like projections with flat ends adhering to the solid substratum; the perisarc gradually thins out distally; on thinner perisarc region there can be a few thick, sharply demarcated perisarc discs used for attachment, but without being associated with notable protrusions of the hydranth wall; further distal some short finger-like protrusions of the hydranth wall can occur.

Blastostyle region of about the same length as foot, provided with numerous (>20-40), widely spaced blastostyles bearing the gonophores and with thin clasper tentacles holding embryos. Blastostyles contractile, hollow and lumen in connection with gastric cavity, stick- to club-shaped (swollen distally), sometimes branched in distal region, distal region provided with nematocyst clusters, these in hemispherical bumps or stubby capitate tentacles with short thick pedicels, quite irregular in appearance; proximal 2/3 of blastostyle with irregularly scattered gonophores, different developmental stages mixed. Gonophores are fixed sporosacs without radial canal system (cryptomedusoid type); males and females occurring on same blastostyle, the animals are thus simultaneous hermaphrodites. Sporosacs spherical, white, female ones larger than male ones, females initially with numerous small oogonia but ultimately only one egg matures. Mature or fertilized eggs leave sporosac but are then grasped by two to five clasper tentacles. Clasper tentacles thin, straight, of variable length, originating in pairs or more at bases of blastostyles or also independently of them, without nematocysts, terminal region sucker-like, enlarged, and attached to the envelope of developing eggs.

Trunk region comprising about half of the animal, capable of great expansion and strong contraction, elongate club-shaped with largest diameter following the blastostyle region, evenly and entirely covered by hundreds of imbricate, indistinctly capitate tentacles; capitate tentacles contractile, hollow, pedicel short in material taken out of the sea (even when anaesthetized, but can extend considerably in undisturbed specimens and become distinctly capitate), capitulum ovoid, diameter not much larger than the contracted pedicel.

The foot and blastostyle parts are less contractile than the trunk. In animals which have been preserved without relaxation, the trunk region is thus only as large or smaller than either the foot and blastostyle region. The long foot is characteristic for this species (comp. Figs 7 and 8-9).

Nematocysts of mature animals: two types of desmonemes, stenoteles, microbasic euryteles. In young polyps, there are also isorhizas (Weill, 1934); they may also be found rarely in adults (own observations).

Colours: living animals entire body, blastostyles, and sporosacs white, capitula of tentacles of trunk purple, perisarc dark amber-brown.



**DIMENSIONS:** Mature body size variable and difficult to establish due to great contractibility, ranging from a few cm to 12 cm, reportedly also more, usually 2-3 cm when contracted; blastostyles up to 4 mm but contractile; capitula of trunk tentacles diameter about 0.2 mm, expanded tentacles up to 2 mm long (Allman, 1874); clasper tentacles 1-2 mm long; diameter of fertilized eggs held by claspers 0.7-0.8 mm, female sporosacs reach same diameter; male sporosacs smaller, 0.30-0.42 mm (Segonzac & Vervoort 1995). Nematocysts of mature animal (preserved material, see Fig. 7F): large desmonemes (12-14) $\times$ (8.5-9.5) $\mu$ m; small desmonemes (7.5-9) $\times$ (5-6) $\mu$ m; stenoteles (11-11.5) $\times$ (8-9) $\mu$ m; microbasic euryteles (18-20) $\times$ (5.5-6) $\mu$ m, ratio of everted shaft to capsule length around 0.9; presumed isorhiza 13.5 $\times$ 5  $\mu$ m.

**BIOLOGY:** Along the coasts of Brittany, fertile animals have been documented from January to September (Teissier, 1965; Castric-Fey, 1970, own data), but likely some animals are reproductive all year round. Asexual reproduction may take place by budding small polyps at the junction of the foot and blastostyle region (Hardy, 1891; Hartlaub, 1916). This asexual budding takes place before the onset of sexual reproduction in early spring (Hardy, 1891).

The animals occur at the spring tide low-water-mark, but records down to 17 m are known (Castric-Fey, 1970; Segonzac & Vervoort, 1995). Sars (1874) gives a depth of 110-146 metres for his record from the Aalesund, which is unusually deep for this animal. Intertidally, the species occurs attached on the underside of large boulders. They can also be attached to holdfasts of laminarians (Castric-Fey, 1970). Billard (1921) made some preliminary observations on their feeding biology. With their much extensible trunk they search their surroundings for small benthic amphipods. It takes about five to six hours to digest one of them. The animals are also able to kill shrimps of up to 2 cm size.

The embryonic development takes place in the embryonic envelope that is held by the clasper tentacles. The animal can thus be considered an actively brooding species. The clasper tentacles only attach to fertilized eggs, as only these form the necessary embryonic envelope (Beigel-Heuwinkel, 1988). The development results in a young polyp with 17-22 tentacles (Billard, 1921). The primary tentacles of the young polyp are only transitory and are replaced by permanent tentacles. More details on the development are given in Allman (1876, as *Myriothele*), Billard (1921), Benoît (1923a, 1925), and van der Vyver (1968).

**ADDITIONAL DATA:** The gastrodermis has numerous folds and villi (cylindrical projections), but has no compartmentalization as in the Tubulariidae (Allman, 1876). The mesogloea is massive and contains thick fibres (Beigel-Heuwinkel, 1982a). It is also involved in the attachment to the substratum (Manton, 1941). Histological details can be found in Allman (1876, as *M. phrygia*) and Hardy (1891, as *M. phrygia*). The tentacles are hollow. Prévot (1959) shows them as closed off to the gastric lumen by a mesogloea lamella, but Allman (1876, pl. 56, fig. 2) states that they are open. An examination of some hand-made cross-sections of the available material showed that there are indeed small openings, but this should be corroborated by more reliable evidence obtained by serial histological sections. The strong contractibility of the tentacles may be regulated by the hydrostatic pressure of the water in the lumen of the



tentacles. If so, an opening to the stomach seems more understandable. The initial tentacles formed while the embryo is still in the egg capsule develop towards the gastric lumen and are only everted at a later stage (Allman, 1876). The primary tentacles must thus have a basal opening. The primary tentacles are quite long and replaced after hatching by shorter tentacles (Allman, 1876).

The sporosacs and their development have been examined by Allman (1876, as *M. phrygia*), Korotneff (1888), Hardy (1891, as *M. phrygia*), Benoît (1923b), and Beigel (1976). Manton (1941) studied the foot and the clasper tentacles. The clasper tentacles were also investigated by Beigel-Heuwinkel (1988). She used light and electron microscopic data to show that the cells at the tip secrete a substance that acts to glue the claspers to the embryonic envelope. Unfertilized eggs do not form an embryonic envelope and are thus not held by the claspers.

Results of regeneration experiments were reported by Billard (1921) and Beigel-Heuwinkel (1982b). Regenerating upper halves of a polyp form no perisarc sheath, but anchoring tentacles as in *C. phrygium*.

**DISTRIBUTION:** North-Eastern Atlantic, absent from the North Sea, Baltic Sea, Mediterranean and Black Sea. The northernmost record is Norway (Aalesund, G. O. Sars, 1874; somewhat doubtful, needs reconfirmation), common in the western English Channel coast of Great Britain and France, also recorded from the Scilly Islands, Isle of Man, western England, southern Brittany, Galicia, Bay of Cadiz (southernmost record) (Segonzac & Vervoort, 1995, Medel & López-González, 1996, this study). Type locality: Gyllyngvase, (Gwyllyn-vase in Cocks, 1850), Falmouth, Cornwall, United Kingdom.

**REMARKS:** *Candelabrum cocksii* has usually been attributed to Vigurs (1849), but that is incorrect. The binomen *Arum cocksii* was introduced in a paper by Cocks that almost certainly appeared in 1850 and not 1849 (Cornelius, 1977). Cocks attributed the name to Vigurs without providing a description. It is thus an invalid name (*nomen nudum*). Furthermore, it seems that Cocks initially did not recognize it as a hydrozoan as he placed it among the Sipuncula. Gosse (1853a: 126) then published the name *Spadix purpurea*, of which Cocks (1853: 365) acknowledged in the same journal that it is identical to his *Arum cocksii*. Cocks (1853) used *Spadix purpurea* as species name followed by *Arum cocksii* in brackets to formalize the synonymy. A suitable description and figures of *Arum cocksii* followed shortly afterwards in Cocks (1854), which made the name formally available for the first time [ICZN, 1999, 4<sup>th</sup> ed., 50.1] [the publication date of Cocks's paper is somewhat unclear, it could be 1853 or 1854; according to Cornelius (1977) it was likely 1854]. Gosse (1853c: 386) acknowledged the synonymy and he apparently ceded his species designation to Cocks by the footnote ".....I gladly recognise, however, the superior claim [of Cocks] of the specific appellation, which pays a deserved compliment to an excellent naturalist."

Although *Spadix purpurea* Gosse, 1853 is likely a senior synonym of *Arum cocksii* Cocks, 1854, the combination *Candelabrum cocksii* (Cocks, 1854) must be taken as valid, this because to my knowledge Gosse's name has not been used as valid after 1899 [ICZN, 1999, 4<sup>th</sup> ed., 23.9.1.1], while *C. cocksii* has been used regularly (see Vervoort & Segonzac, 1995).

*Candelabrum cocksii* (Cocks, 1854) has unfortunately been confounded with *C. phrygium* (Fabricius, 1780) by Hincks (1868), Allman (1876), and many subsequent authors relying on Hincks (see Vervoort & Segonzac (1995) for synonymy and misidentifications). Recently, Cornelius (1977) again maintained that both are conspecific. Cornelius based his claim by referring to other authors, e. g. Stechow (1923) and Teissier (1965). These two authors, however, do not claim such a synonymy, and Stechow even advocates a separation at the genus level. The opinion of Cornelius is also not shared by Segonzac & Vervoort (1995) as well as by the present author. Both species are clearly separable. *Candelabrum cocksii* and *C. phrygium* differ in the foot morphology (long, perisarc covered foot versus short, naked one); clasper tentacles (presence versus absence), and the sexual reproduction (hermaphroditic versus gonochoristic).

The tentacles of the trunk are usually short and only indistinctly capitate, this in preserved material as well as in living material taken into the laboratory. The tentacle pedicels are very contractile and undisturbed animals have quite long tentacles (2 mm; Allman, 1874). This has also been observed for the closely related species *C. serpentarii* (see figs 3A-B in Segonzac & Vervoort, 1995). *Candelabrum serpentarii* Segonzac & Vervoort, 1995 is only known from deep waters of the central Atlantic. This species is also monoecious, but lacks clasper tentacles and its eggs are four to five times larger. The only *Candelabrum* species that also has clasper tentacles is the Pacific *Candelabrum fritchmanii* Hewitt & Goddard, 2001. This species can form colony-like aggregates, a unique feature within this genus.

### ***Candelabrum phrygium* (Fabricius, 1780)**

Fig. 8

*Lucernaria phrygia* Fabricius, 1780: 343.

*Myriothele arctica* M. Sars, 1850: 14.

*Myriothele phrygia* – Sars, 1877: 23, pl. 2 figs 29-36; Bonnevie, 1899: 35, pl. 4 figs 5-6; Jäderholm, 1908: 9, pl. 1 fig. 7; Broch, 1916: 19, fig. C, pl. 1 figs 3 & 8; Rees, 1957: 486, fig. 36; in part Naumov, 1969: 261, not figures; Calder, 1972: 222, pl. 1 fig. 5.

? *Myriothele gigantea* Bonnevie, 1898a: 490, pl. 27 figs 46-47; Bonnevie, 1899: 38, pl. 4 fig. 1.

? *Myriothele minuta* Bonnevie, 1898a: 489, pl. 27 fig. 44; Bonnevie, 1899: 37, pl. 3 fig. 6a-b, pl. 4 fig. 4.

? *Myriothele mitra* Bonnevie, 1898a: 489, pl. 27 fig. 43; Bonnevie, 1899: 38, pl. 3 fig. 6c-e, pl. 4 fig. 3.

*Candelabrum phrygium* – in part Cornelius 1977: 521 [excl. synonymy]; Segonzac & Vervoort, 1995: 45, figs 2e-f, 3E-F, table 1 [some references do not refer to this species]; Schuchert, 2001a: 37, fig. 24.

**MATERIAL EXAMINED:** Re-examined material mentioned in Schuchert (2001a), ZMUC, Greenland, no exact locality and date known, collected by Lüthken, identified by P. Kramp, two specimens, both broken into two parts, one obvious female on branching bryozoan (Cellariidae), other animal on red algae, previously identified as male; one blastostyle of both specimens was used for serial histological sections, both specimens proved to have female sporosacs only, though the tissue preservation is not good. – All suitable material found in the BMNH that is labelled as *C. phrygium* turned out to be *C. cocksii*.

**DIAGNOSIS:** *Candelabrum* species without clasper tentacles, dioecious, basal foot short or absent, straight and not sheathed in perisarc envelope, attached to substratum by tentacle-like filaments usually ending in perisarc discs.

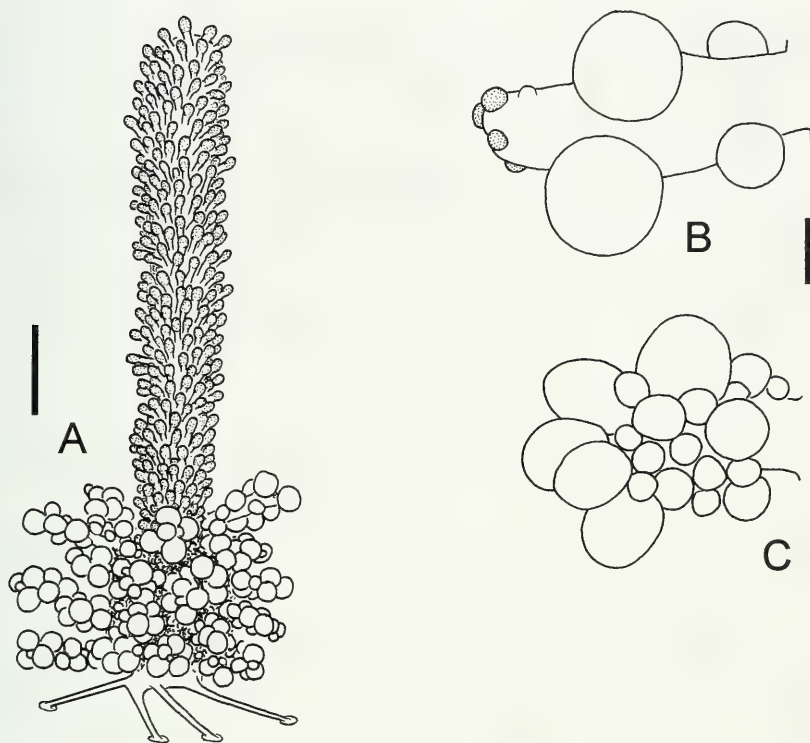


FIG. 8

*Candelabrum phrygium* (Fabricius, 1780), after preserved material from Greenland. A) Entire polyp, scale bar 2 mm. B-C) Blastostyles, scale bar 0.5 mm.

**DESCRIPTION** (after Sars, 1877; Segonzac & Vervoort, 1995; own data): Polyp solitary, worm-like, size very variable as able to expand and contract enormously. Hydranth shape also variable, usually cylindrical to conical, subdivided into a distal tentaculate region (trunk), followed by a blastostyle region and sometimes also a foot zone.

Foot zone either very short in relation to other parts or absent, not curved, adhering to substratum by several tentacle-like attachment filaments, each of them with terminal region sucker-like and enlarged, attached to a perisarc disc that adheres to substratum, perisarc discs sometimes absent.

Blastostyle region about 1/4 to 1/3 of contracted polyp, beset by many (>20) club-shaped blastostyles. At distal end of blastostyles four to six nematocyst clusters in wart-like tubercles. Blastostyles bear sessile sporosacs, the two sexes on different polyps, sporosacs without nematocyst tubercles. Male sporosacs spherical, without radial canals, up to 50 per blastostyle at different developmental stages. Females with two to six sporosacs per blastostyle, maximally two mature, others in development, spherical, no radial canals, initially many eggs but presumably only one egg per sporosac attains maturity, fertilized in situ and developing into a young polyp, hence viviparous.



Trunk region comprising majority of hydranth length, with numerous (>200) capitate tentacles, these hollow, extensible, capitula ovoid.

Colours: cream-white. Nematocysts: stenoteles; ? haplonemes; desmonemes of two size classes.

**DIMENSIONS:** Height of contracted specimens 2-6 cm, expanded up to 30-40 cm (Bonnievie, 1899; Broch, 1916), width a few mm. Diameters of male sporosacs 0.4-0.8 mm when mature, females 0.9-1.4 mm. Capitate tentacles with stalk 0.3-0.5 mm, capitula 0.17-0.25 mm (Segonzac & Vervoort, 1995). Nematocysts (Segonzac & Vervoort, 1995): stenoteles  $(10.6-11.5) \times (8.2-9.8) \mu\text{m}$ ; ? haplonemes  $(19.7-20.5) \times (8.2-9.9) \mu\text{m}$ ; desmonemes of two size classes  $(12.5-13.0) \times (9.0-9.8) \mu\text{m}$  and  $(8.2-9.0) \times (6.4-6.6) \mu\text{m}$ .

**BIOLOGY:** Occurs usually at considerable depths of several hundreds of meters down to 2195 m (Bonnievie, 1899), but in the high Arctic it has been found as shallow as 13 m (Jäderholm, 1908). The polyps live permanently attached to solid substrata like rock, bivalves, hydroids, bryozoans, and algae. The animals are viviparous and lack a planula phase (Sars, 1877; Schuchert, 2001a); the newly released polyp is spherical and has 20-30 capitate tentacles. The tentacles formed while the embryos are still in the egg capsule develop inverted into the gastric lumen, but evert before hatching.

**DISTRIBUTION:** An Arctic, deepwater species penetrating into boreal regions, in European waters reaching as far south as the Trondheimfjord and the Wyville-Thomson-Ridge between Scotland and The Faeroes (Broch, 1903; Broch, 1916). Segonzac & Vervoort (1995) report a find from the Mid-Atlantic Ridge south-west of the Azores in a depth of 1622 m, which is the southernmost record of this species. It has also been recorded in northern Norway (Sars, 1877; Bonnievie 1899), Jan Mayen (Broch, 1916), Russian Arctic Seas (Jäderholm, 1908; Naumov, 1969), northern Pacific (Naumov, 1969). Also known from Iceland (Broch, 1916), Greenland (Schuchert, 2001a), Canada (Calder, 1972). (Note that numerous other records under this name from coastal regions of the NE Atlantic refer in fact to *Candelabrum cocksii*). Type locality: Greenland.

**REMARKS:** The synonymy of this species has been worked out quite thoroughly (Sars, 1877; Bonnievie, 1899; Segonzac & Vervoort, 1995). *Myriothele arctica* Sars, 1850 was synonymized by Sars himself after he had re-examined Fabricius' type material (Sars, 1877). The boreal shallow-water species *Candelabrum cocksii* has often been synonymized with this species, but this is not tenable (see under *C. cocksii*). Some of Bonnievie's *Candelabrum* species (*C. minutum*, *C. mitra*, *C. giganteum*) are not well characterized and might also belong to this species (Rees, 1956). They are here listed as questionable synonyms (see also Segonzac & Vervoort, 1995). The material on which these three species were based, already fragmentary when examined by Bonnievie (1899), is now in such a bad condition that it is virtually useless (Rees, 1956). Contrary to the view of Rees (1956), *Candelabrum verrucosum* (Bonnievie, 1898) is well characterized and it is re-described below.

*Candelabrum phrygium* is portrayed as being dioecious, but for preserved material it is often difficult or impossible to determine the sex. This is easy only for



well advanced female sporosacs as they contain young polyps. For a reliable sex determination, serial histological sections must be made. One blastostyle of each of the two specimens examined for this study was thus used to make serial sections. Both animals had female sporosacs only. One specimen did not have sporosacs with advanced embryos and was thus initially mistaken for a male (Schuchert, 2001a). This shows that sex identifications of preserved material are often unreliable. More investigations using histological sections of entire blastostyles are desirable to confirm that *C. phrygium* is always dioecious (comp. *C. verrucosum*).

The material examined in this study and also by other authors (Sars, 1877) had attachment tentacles that were cemented to the substratum by distinct perisarc discs that adhere tightly to the substratum and cannot be removed without destroying them. Dislodged hydranths lack them regularly. Sometimes they are quite thin and inconspicuous and if attached on rock they might be hardly visible. This could explain that some investigators did not find them (e. g. Segonzac & Vervoort, 1995), but is well possible that they can also be absent.

***Candelabrum verrucosum* (Bonnievie, 1898)**

Fig. 9

*Myriothele verrucosa* Bonnievie, 1898a: 468, pl. 27 fig. 45; Bonnievie, 1899: 37, pl 4, fig. 2.

*Candelabrum verrucosum* – Segonzac & Vervoort, 1995: 53.

MATERIAL EXAMINED: ZMUC, Kap Farvel expedition station 148, 60.07°N 43.20°W (Greenland), 50 m, 27 August 1966, from rocky bottom, fertile female with sporosacs containing embryos, tissues somewhat shrunken. Two blastostyles were used to make serial histological sections, confirming the presence of male and female sporosacs.

DIAGNOSIS: *Candelabrum* species with sporosacs bearing scattered nematocyst buttons on their surface, monoecious, no clasper tentacles; foot straight, not covered by perisarc, attached via attachment filaments; size 1–4 cm.

DESCRIPTION (after examined specimen): Solitary polyp, 1.1 cm, cylindrical, divided into three regions: distal tentaculate region (trunk), followed by a blastostyle region and a foot zone.

Foot zone about 1/6 of animal, straight, with several (>10) tentacle-like attachment filaments of variable length, some of them with enlarged, sucker-like ends; one filament with terminal perisarc disc, those of other filaments presumably lost.

Blastostyle region taking up about half of the polyp, bearing many (>20) club-shaped blastostyles, clasper tentacles absent. Nematocyst clusters in wart-like tubercles at distal end of blastostyles. Blastostyles bear several (up to 8) sessile sporosacs. Sporosacs with up to eight distinct nematocyst buttons on surface, no radial canals or ring canals present. Largest sporosacs contain a single young polyp, animal thus viviparous. Besides female sporosacs, there is also one male sporosac per blastostyle, animals thus simultaneous hermaphrodites.

Trunk region about 1/3 of hydranth length, covered by numerous (>100) capitate tentacles, their capitula ovoid.

Nematocysts (not well preserved): stenoteles, large desmonemes, ? heteronemes.

DIMENSIONS: Hydranth can reach 4 cm (Bonnievie, 1898a), sporosacs up to 0.9 mm, blastostyles up to 2.2 mm, diameter of capitula 0.2 mm.



FIG. 9

*Candelabrum verrucosum* (Bonnevie, 1898), after preserved material from Greenland. A) Whole animal, the blastostyle region covers slightly more than half of the animal, note the nematocyst buttons on the sporosacs, scale bar 2 mm.

ADDITIONAL DATA: The tentacles formed while the embryos is still in the egg capsule develop inverted into the gastric lumen, but evert before hatching.

DISTRIBUTION: Northern Norway, Southern Greenland (this study). Type locality: Norway, Hammerfest (Bonnevie, 1899).

REMARKS: *Candelabrum verrucosum* (Bonnevie, 1898) has hitherto been known from one specimen described by Bonnevie (1898a, 1899). Some authors doubted its validity and thought it might belong to *C. phrygium* (e. g. Rees, 1956). The species is characterized by sporosacs that bear scattered buttons of nematocyst clusters. This is quite a unique feature and has never been observed for *C. phrygium*. I am convinced that *C. verrucosum* is a valid species, distinct from *C. phrygium*, and that the material described above belongs to it. The characteristic nematocyst buttons on the sporosacs are quite conspicuous in material examined with a dissecting microscope. There are a few discrepancies from the original material described by Bonnevie (1898a): there are more than two sporosacs per blastostyle, the blastostyle region is larger, and the animal is smaller. As these traits show considerable intraspecific variation in other *Candelabrum* species, they are here also considered as such.

*Candelabrum verrucosum* is easily distinguished from *C. phrygium* by the nematocyst buttons on the sporosacs, but it differs additionally by being monoecious. Otherwise, both species are very similar. Only two blastostyles could be used to make serial histological sections. Both blastostyles had female sporosacs of all develop-

mental stages (some containing almost fully formed young polyps) and a single male sporosac filled with spermatids. The male sporosacs are smaller than the female ones.

Genus *Monocoryne* Broch, 1910

TYPE SPECIES: *Coryne gigantea* Bonnevie, 1898b.

SYNONYMS: *Symplectanea* Fraser, 1941 (see Rees, 1958).

DIAGNOSIS: Hydroid solitary or a few polyps in loose aggregates that may have a common perisarc base. Hydranth long, cylindrical, divided into tentaculate body and foot region. Foot covered by thin perisarc, with root-like attachment processes. Hydranth body with scattered capitate tentacles, at least some of them compound tentacles, i.e. branched tentacles with a common epidermis at the base, bases of the side-branches adnate to the side of the main tentacle for some distance, all ends capitate. Gonophores fixed sporosacs developing directly on hydranth body, associated or not with tentacles.

REMARKS: For more details consult Rees (1956, 1958), Petersen (1990), or Stepanjants *et al.* (2003). The European fauna comprises one species only. Stepanjants *et al.* (2003) give an overview on all species.

*Monocoryne gigantea* (Bonnevie, 1898)

Fig. 10

*Coryne gigantea* Bonnevie, 1898b: 4, pl. 1 fig. 1.

*Monocoryne gigantea* – Broch, 1910: 138; Broch, 1916: 12, pl. 1 fig. 1; Johannesen, 1924: 1, figs 1-7, pl. 1-2; Rees, 1956: 117, figs 1-2; Rees, 1957: 488, fig. 38; Calder, 1972: 222, pl. 1 fig. 4; Antsulevich, 1988: 931, fig'd; Petersen, 1990: 203; Stepanjants *et al.*, 2003: 100, figs 1A-F, 6.1.

DIAGNOSIS: *Monocoryne* species up to 15 mm; compound tentacles with two to four capitate ends, usually three; hermaphroditic, sporosacs in upper axils of compound tentacles.

DESCRIPTION: (after Bonnevie, 1898b; Johannesen, 1924; Rees, 1956; Stepanjants *et al.*, 2003) Vermiform hydranths, solitary or clustered into loosely joined aggregates, attached laterally to substratum by curved proximal end; divisible into foot (caulus) zone and tentaculate part. Foot roughly 1/2 of total length, covered by close fitting, soft, thin perisarc, in lower half of foot several large, distinct anchoring filaments with widened distal end. Tentaculate part also about 1/2 of length, but very extensile and active in life, all tentacles distinctly capitate with spherical capitula, very extensible, around mouth about eight simple capitate tentacles, below them many (< 30) scattered compound tentacles and also some simple ones. Compound tentacles usually with three, sometimes two or four capitate ends, with middle branch(es) thickest and longest, the side-branches originate near its base and are adnate for some distance before they become free, the fused part forming a plate-like base with a common epidermis. Gonophores sessile sporosacs arising in the upper axils of the compound tentacles, sporosacs oblong, without radial canals; male, female and hermaphroditic sporosacs can be produced by the same animal (Broch, 1916; Johannesen, 1924). Nematocysts: stenoteles, microbasic mastigophores, desmonemes, microbasic euryteles.

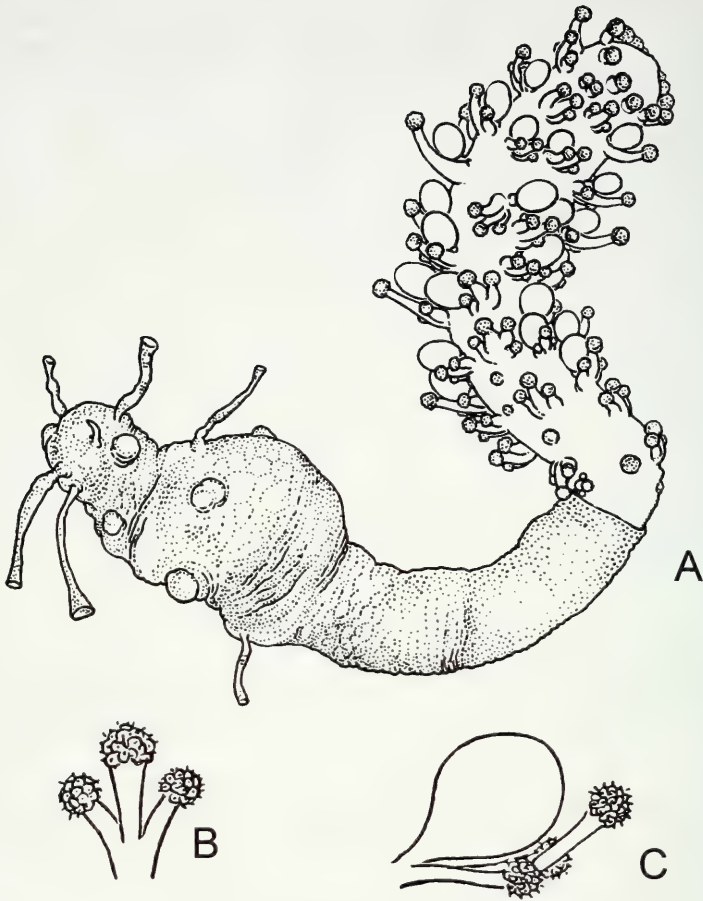


FIG. 10

*Monocoryne gigantea* (Bonnevie, 1898), modified from Rees (1956). A) Whole polyp, foot with perisarc stippled dark. B) Compound tentacle. C) Side view of sporosac in axil of compound tentacle.

**DIMENSIONS** (Rees, 1956; Stepanjants *et al.*, 2003; consult these references for additional measurements): Fertile polyps 11-15 mm (preserved material), diameter of hydranth body 1.4-1.7 mm, length of gonophores 0.6-0.9 mm, diameter 0.4-0.5 mm. Nematocysts: stenoteles (14-18)x(12-18)  $\mu\text{m}$ ; microbasic mastigophores (19-24)x(8-11)  $\mu\text{m}$ ; desmonemes 10x8  $\mu\text{m}$ , microbasic euryteles (22.5-25)x(12-12.5)  $\mu\text{m}$ .

**BIOLOGY:** A rare species, occurs usually in waters of 100 m depth and more, but in the high Arctic archipelago Franz Joseph Land it was found in only 16-20 m (Antsulevich, 1988). Known substrata (Svenander, 1904) are a *Tubularia* spec. and polychaete tubes, both attached on shells of the bivalve *Lima excavata*.

**DISTRIBUTION:** Arctic species, with its southern limit in the Trondheimsfjord (Johannesen, 1924). It has been recorded from northern Norway (Bonnevie, 1898b),



Franz Joseph Land (Antsulevich, 1988), North-Eastern Canada (Calder, 1972). Type locality: Hammerfest, Norway.

REMARKS: Rees (1958) synonymized the genera *Symplectanea* and *Monocoryne*, but kept *M. bracteata* provisionally distinct from *M. gigantea* because of its larger size and the greater number of capitate heads per compound tentacles, but he suggested that more material might show it to be synonymous with *M. gigantea*. It could be that *Monocoryne bracteata* is dioecious, thus differing from the monoecious *M. gigantea*. The only other named species of the genus is *Monocoryne minor* Millard, 1966. It is smaller and its sporosacs develop independently of the tentacles.

#### FAMILY TRICYCLUSIDAE KRAMP, 1949

DIAGNOSIS: Solitary, usually benthic hydroids, having a conical to pear-shaped hydranth and tapering pedicel ending in a small attachment disc. Pedicel covered in a loose, filmy or gelatinous perisarc. Tentacles in three whorls, one oral whorl, one in middle of hydranth body, and one near base of body. Oral tentacles capitate, other tentacles also capitate but bearing additional nematocyst clusters. Vegetative budding of hydranths below proximal tentacles. Gonophores develop above proximal set of tentacles and remain fixed. Male gonophores medusoid, with radial canals and circular canal. Female ones without canal system. Cnidome: Stenoteles, desmonemes, and heteronemes.

#### Genus *Tricyclusa* Stechow, 1919

TYPE SPECIES: *Tiarella singularis* Schulze, 1876.

SYNONYM: *Tiarella* Schulze, 1876.

DIAGNOSIS: As for the family.

REMARKS: The genus *Tricyclusa* is currently monotypic, containing only *Tricyclusa singularis* (Schulze, 1876). Schulze (1876) originally proposed the genus name *Tiarella* for this species. Because this name is preoccupied for a gastropod and also other taxa, Stechow (1919: 6) proposed the new name *Tricyclusa*. It is a characteristic genus and it poses no taxonomic problems.

#### *Tricyclusa singularis* (Schulze, 1876)

Fig. 11

*Tiarella singularis* Schulze, 1876: 415, pls 29-30; Bedot, 1911: 209, pl. 11 fig. 2.

*Tricyclusa singularis* – Stechow, 1919: 6; Rees, 1941: 133, fig. 3; Rees, 1957: 462, 505, figs 6 & 51B; Picard, 1957: 10; Ververs, 1959: 506, figs 1-6; Teissier, 1965: 10; Bouillon, 1974: 142; Petersen, 1990: 146, fig. 15; Bouillon *et al.*, 2004: 103, fig. 55D.

*Margelopsis stylostoma* Hartlaub, 1903: 28, fig. 2; Hartlaub, 1907: 91, fig. 87; Bedot, 1911: 211; Rees, 1941: 133.

MATERIAL EXAMINED: BMNH 1957.6.26.1-10, Roscoff intertidal, leg. Cantacuzène, on red algae, numerous well preserved specimens. – BMNH 1956.11.7.7-13, Baie de Morlaix, 23 June 1955, coll. W.J. Rees, on *Chorda filum*, several contracted specimens.

DIAGNOSIS: As for the family.

DESCRIPTION (after literature and observed material): Hydroid solitary, usually attached to algae, sometimes freely floating, divided into hydranth body and pedicel,

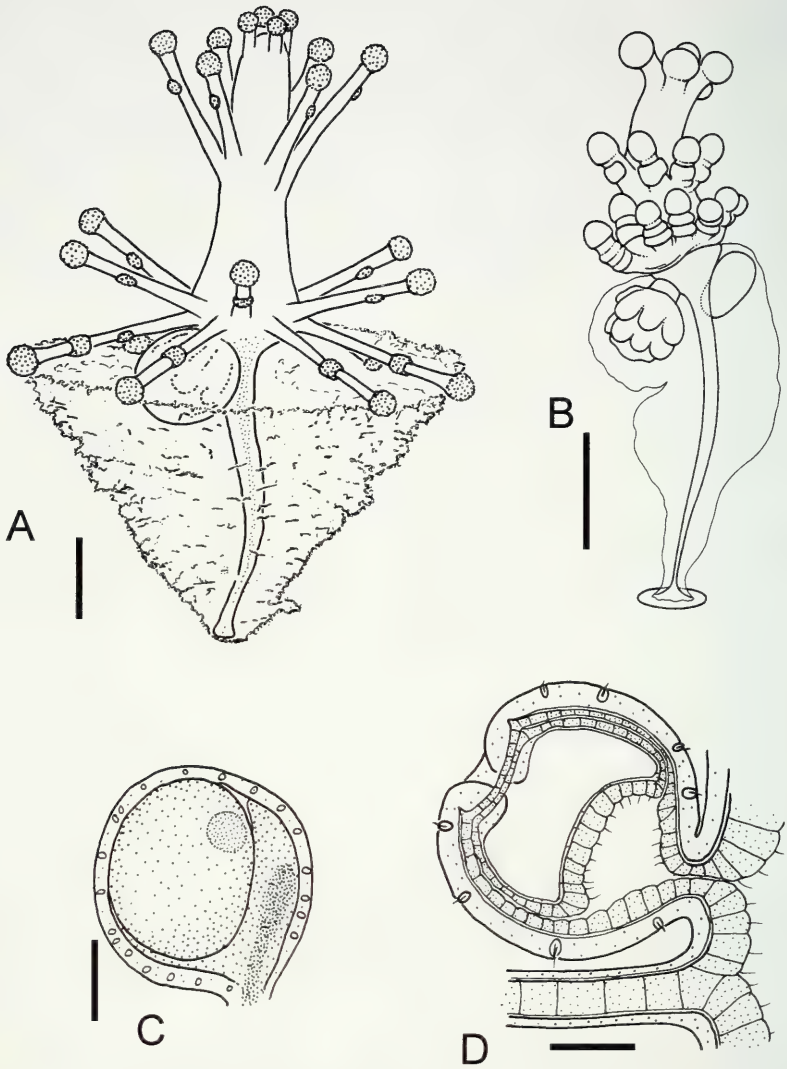


FIG. 11

*Tricyclusa singularis* (Schulze, 1876), after preserved material. A) BMNH 1957.6.26.1-10, Roscoff, polyp with long tentacles, scale bar 0.2 mm. B) polyp with short tentacles, after Petersen (1990), scale bar 0.5 mm. C) Optical section of a female sporosac, modified after Bedot (1911), scale bar 0.2 mm. D) Optical section of a male medusoid after it has liberated its gametes, modified after Schulze (1876), scale bar 0.05 mm

both of about the same length. Pedicel in a conical, loose, filmy or gelatinous periderm cup, wrinkled, with adhering detritus particles. Pedicel tapering proximally, ending at base in a small attachment disc. Hydranth pear-shaped to conical, broadest near lower end, with three distinctly separated sets of tentacles, tentacle gastrodermis chordoid. Oral tentacles in one whorl, four to five in number, short, capitate, directed upwards;

middle whorl of tentacles approximately in middle of body, usually six in number, directed obliquely upwards, with terminal nematocyst knob and with or without additional one to two knobs in distal half of tentacle; basal tentacles 10 to 14, usually 12, in two closely approximated whorls, alternately pointing up- and downwards, with terminal knob and additionally one or more proximal knobs, these either clasping or encircling tentacle. Underneath lowest tentacles vegetative polyp buds, one to six in number, budded polyps are released as small, fully formed hydranths but have a short pedicel, newly released polyps may already have incipient gonophores. Gonophores develop immediately above basal whorl of tentacles, spherical, remaining attached to hydroid. Male gonophores with four radial canals and ring canal, thus of medusoid type. Female gonophores sporosacs without canal system, with one large egg. Nematocysts: Stenoteles, desmonemes, microbasic euryteles.

**DIMENSIONS:** Total height around 2 mm, hydranth about 1 mm high, hydranth base diameter 0.4-0.6 mm. Female sporosacs after Bedot (1911) about 0.6 mm, male medusoids after Schulze (1876) about 0.2 mm.

**ADDITIONAL DATA:** The length of the tentacles is variable, and this is not only due to contraction. Young individuals and polyps found in the plankton have very long and thin tentacles that get shorter once the animal attaches itself (Bedot, 1911). Young animals and those from the plankton also have a short pedicel.

**DISTRIBUTION:** Adriatic Sea, Northern Brittany, western Ireland. Type locality: Adriatic Sea, Trieste, Bay of Muggia (Italy), on *Cystoseira*.

**BIOLOGY:** The polyps live attached to various macroalgae and *Zostera* plants near the low-water-mark (Rees, 1941, Teissier; 1965). Occasionally, detached polyps can be found in the plankton, but this is not the usual mode of life (Bedot, 1911). In Brittany it occurs mainly from May to July, although some animals were also found during March and April (Bedot, 1911; Teissier, 1965). In the Mediterranean it was found in April (Schulze, 1876). The fertile period for Brittany is from May to June (Bedot, 1911; Teissier, 1965). It is a rare species, but when present, it can occur in large numbers (Bedot, 1911).

**REMARKS:** *Tricyclusa singularis* (Schulze, 1876) is a characteristic and unproblematic species. Hartlaub (1903, 1907) described a similar species from the plankton of Roscoff which he named *Margelopsis stylostoma*, differing mainly only in the short pedicel. Even Hartlaub (1903, 1907) suspected that it was only a planktonic form of *Tricyclusa singularis*. It was later synonymized with *Tricyclusa singularis* by Bedot (1911) and Rees (1941).

Although easy to identify and despite its presence near the water surface, this animal has only rarely been reported. After its discovery, it has never been found again in the Mediterranean Sea. It seems that it is only occasionally present and quite seasonal. Most regularly it has been seen at Roscoff (Brittany). It is particularly interesting to note that it has never been reported from the other side of the English Channel, despite England being one of the best investigated regions. Perhaps it prefers warmer waters, an assumption also underlined by its occurrence during the summer months. Probably it survives unfavourable conditions through a sexually produced resting stage.

FAMILY **MARGELOPSIDAE** UCHIDA, 1927TYPE GENUS: *Margelopsis* Hartlaub, 1897.SYNONYM: *Pelagohydridae* Dendy, 1902.

DIAGNOSIS: Hydroid solitary, pelagic; hydrocaulus absent or reduced to a small process; hydranth body vasiform, tentacles filiform to moniliform, arranged into two separate sets, oral tentacles in one or several whorls; aboral tentacles either in two to three alternating whorls or numerous and scattered over most of body. Gonophores free medusae, medusa buds develop among tentacles or above aboral tentacles.

Medusa manubrium with simple mouth; gonads surrounding manubrium entirely; four radial canals; tentacles solid, generally moniliform, two or more tentacles per marginal bulb, in some genera tentacles also issuing at different levels on exumbrella; without ocelli.

REMARKS: With its clustered marginal tentacles in the medusae and the pelagic polyps, this is a distinct and characteristic family of the Capitata. It comprises the genera *Climacocodon* Uchida, 1924, *Margelopsis* Hartlaub, 1897, and *Pelagohydra* Dendy, 1902 (Petersen, 1990). The well established and frequently used name Margelopsidae Uchida, 1927 is threatened by the senior synonym Pelagohydridae Dendy, 1902. The latter name has not been used and for the sake of nomenclatural stability it is preferable to continue to use Margelopsidae. According to the ICZN [article 29.3.1.1] there is no need to change it to the formally correct Margelopsididae.

## KEY TO GENERA:

- 1a medusa with several tentacle pairs on exumbrella ..... *Climacocodon* (not in European fauna)
- 1b medusa tentacles in four groups along bell margin: ..... 2
- 2a polyp with caulus rudiment, aboral tentacles in two to three close whorls . . . *Margelopsis*
- 2b polyp without caulus rudiment, aboral tentacles scattered ..... *Pelagohydra* (not in European fauna)

***Margelopsis* Hartlaub, 1897**TYPE SPECIES: *Margelopsis haeckelii* Hartlaub, 1897 by monotypy.

DIAGNOSIS: Hydroid with hydrocaulus rudiment, without parenchymatic specializations of the gastrodermis; tentacles indistinctly moniliform; oral tentacles in one whorl, aboral ones in two to three whorls, medusae buds above aboral tentacles.

Medusa with four perradial tentacular bulbs on bell margin, each with two to six solid tentacles.

REMARKS: There are two species of *Margelopsis* in the European fauna, namely *Margelopsis haeckelii* and *M. hartlaubii*. See the diagnoses for ways to distinguish them.

***Margelopsis haeckelii* Hartlaub, 1897**

Figs 12-13

*Margelopsis Haeckelii* Hartlaub, 1897: 482, pl. 16b figs 12-18; Hartlaub, 1899: 219, figs 1-3 [hydroid].

*Margelopsis haeckeli* – Hartlaub, 1907: 89, 91, figs 84-86; Müller, 1908: 43, pl. 4 figs 12-17, pl. 5 figs 18-19; Mayer, 1910: 80, fig. 38; Leloup, 1930: 97, fig.; Kramp, 1930: 12; Kramp, 1937: 32, fig. 10; Thiel, 1938: 294; Leloup, 1946: 1; Russell, 1953: 95, figs. 41A-C,



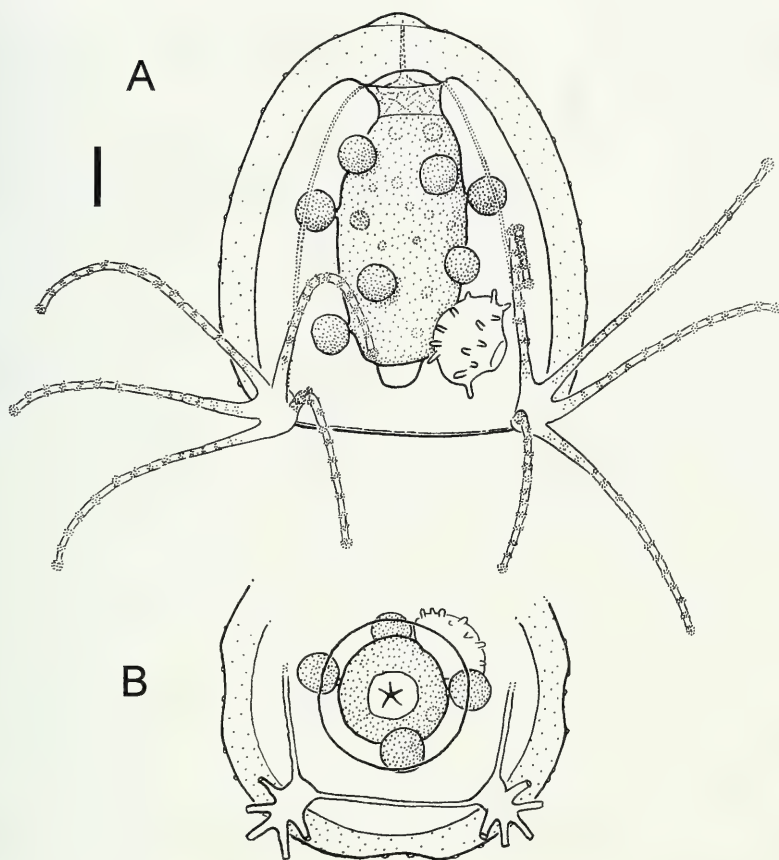


FIG. 12

*Margelopsis haeckelii* Hartlaub, 1897; schematic pictures derived from various preserved samples. Mature medusa with subitaneous eggs and one young polyp, scale bar 0.3 mm. B) Oral view of a medusa, tentacles clipped, same scale as A.

42A-B; Werner, 1954: 124, figs 1-9; Werner, 1955: 1-30, figs 1-9; Prévot, 1959: 104, pl. 3 fig. 11; Kramp, 1959: 92, fig. 47; Kramp, 1961: 49; Russell, 1970: 234; Bouillon, 1974: 143.

**MATERIAL EXAMINED:** BMNH 1967.5.25.1-8, Helgoland, 12 May to 24 July 1958, medusae and polyps. – BMNH 1967.5.25.6, 2 medusae from Sylt, 10 July 1958, with resting eggs. – Zoological Museum Hamburg, about 50 mature medusae, collected in plankton by B. Werner, 24 July 1958, with subitaneous and resting eggs. – Zoological Museum Hamburg, several polyps from List, collected 27 June 1961, cultivated by B. Werner, with medusae buds.

**DIAGNOSIS:** *Margelopsis* polyp with vasiform body, stalk rudiment, two well-separated sets of tentacles, medusae buds in one whorl oralward of aboral tentacles. Medusae of up to 2 mm high, umbrella bell-shaped, moderately thick, apical canal present, 3-6 tentacles per bulb, manubrium base with large vacuolated cells, usually only females present, eggs of two types: subitaneous eggs developing directly into polyp stage, diapausing eggs developing first into encysted resting stage.

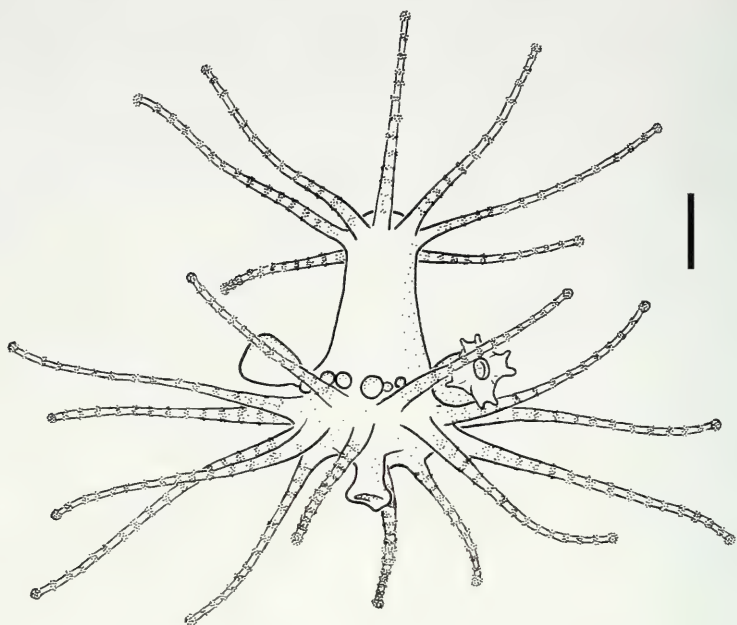


FIG. 13

*Margelopsis haeckelii* Hartlaub, 1897; schematic picture derived from various preserved samples. Polyp with medusae buds, oral side above, scale bar 0.2 mm.

**DESCRIPTION** (after examined material and literature): Newly released polyps actinula-like, ovoid, with short tentacles, tentacles numbers slightly lower than in fully mature animals.

Mature polyp planktonic, body vase-shaped, resembling a detached tubularian hydranth, at aboral end a short stalk rudiment with a central depression. Tentacles in two well-separated sets, rather stiff, with nematocysts concentrated in rings and a small terminal knob, base of tentacles free of nematocysts. Aboral tentacles slightly longer than oral ones, 12-15 in two closely approximated whorls, alternately pointing obliquely up- and downward. Oral tentacles around short conical hypostome, five to eight in number. Medusae buds borne on body of hydranth just oralward of the aboral tentacles, sometimes groups of medusa buds on a short stalk. Medusae develop without envelope, the tentacles are free and not tucked into the subumbrella as in most other hydromedusae.

Umbrella of very young medusae relatively wider than in adult, apical jelly thin, nematocysts evenly scattered over exumbrella; broad umbilical canal, stomach length less than half the height of subumbrellar cavity, a circle of nematocysts surrounds the mouth-opening, without gonads. Four radial canals and ring-canal narrow. Four perradial marginal bulbs each with two to three tentacles. Tentacles covered with scattered clusters of nematocysts, but base of tentacles without nematocysts. Umbilical canal and marginal bulbs with black pigment. Umbrella becomes higher with further

growth. In a specimen 1.5 mm high, apical jelly considerably thicker than sides of umbrella, many exumbrellar nematocysts, umbilical canal has narrowed, stomach considerably longer. Upper third of stomach without gonads, with large gastrodermal cells covered by thin layer of epidermis. Gonad covering lower two-thirds of the stomach thin. Three to four tentacles irregularly placed on each marginal bulb, with irregularly scattered nematocysts which appear as ring-like bands when tentacle contracted. Upper basal third of stomach clear and transparent in contrast to opaque brownish grey appearance of lower part.

Adult medusa with bell-shaped umbrella, slightly higher than wide, without apical process or with small apical process; with scattered exumbrellar nematocysts; jelly moderately thick, thicker at apex, velum moderately broad to narrow. Stomach cylindrical, length  $2/3$  to  $1/1$  of subumbrellar height; basal portion with large transparent gastrodermal cells; apical canal regularly present (rest of umbilical canal); mouth simple, circular, margin armed with nematocysts. Four radial canals and ring canal narrow. Gonad surrounding stomach, leaving upper third free. Eggs amoeboid, embryos developing attached to manubrium on pedicel, depending on season either into young polyp or encysted resting stage. Four perradial rounded marginal bulbs, each with four to seven somewhat stiff tentacles, usually irregularly radiating, with nematocysts concentrated in rings and a small terminal knob, thus nearly moniliform, gastrodermal cells chordoid. No ocelli. Colour of stomach dark grey with dark brown pigment granules; marginal bulbs brown. Nematocysts desmonemes, basitrichous haplonemes, microbasic euryteles, stenoteles.

**DIMENSIONS:** Adult medusa up to 2 mm high, subitaneous egg production starts at a bell diameter of 1-1.5 mm and with 3-5 tentacles per bulb, resting eggs are produced by full sized animals only; subitaneous eggs 0.12-0.13 mm, resting eggs 0.18-0.21 mm; newly released medusa 0.5 mm; newly released polyp resulting from subitaneous eggs 0.3-0.4 mm, adult polyps 1-2 mm (Werner, 1954), aboral tentacles as long as hydranth or slightly longer.

**BIOLOGY:** Polyps and medusae are usually present in the plankton from June to September, but they have also been seen earlier. They are thought to remain floating through water currents, as they sink in still water. Their numbers fluctuate drastically from year to year. Werner (1954, 1955) made detailed investigations on the life history and development of this species. Male medusae appear to be extremely rare; Werner (1954) observed only one hermaphrodite in 250 medusae, the others being all female. The immature eggs are amoeboid and grow by engulfing other eggs (Müller, 1908). The eggs develop parthenogenetically (Werner, 1956). Two different types of eggs are produced: smaller subitaneous eggs and larger resting eggs. Both egg types start their development attached to the manubrium by a small stalk. The total production of subitaneous eggs depends on the food availability of the medusa and varies in number from a few eggs to 30 or 40. For the most part, only two to three egg cells mature and emerge at the same time. Often a medusa bears 20-30 eggs and embryos on the manubrium, of different ages and different developmental stages. The subitaneous eggs are produced earlier when water temperatures are between 7 and 15°C. They develop directly within four to ten days into a small polyp that is then released from the medusa. Later in the



year, when water temperatures exceed 15°C, the production of subitaneous eggs stops and resting eggs are produced. These are larger than the subitaneous eggs and possess nematocysts on their surface. Generally, only one or two of this type are formed at the same time and usually not more than six of them remain attached to the manubrium. The initial development takes place when the egg is attached to the manubrium and reaches a 'stereo-blastula' stage (a thin layer of ectodermal cells surrounds a mass of yolky endodermal cells). At this stage development stops, the egg detaches and sinks to the bottom, where it may attach or not as a lens-shaped cyst. The nematocyst layer helps in the attachment process. The embryo forms a periderm capsule with a characteristic polygonal pattern. The animal overwinters then as a cyst and after 6-9 months a small polyp hatches in the next spring (Werner, 1984). The newly released polyp lives in the plankton where it grows to full size and then produces medusae.

It seems that only few resting stages survive the winter, as initially there are only very few hydroids in the plankton. However, through the following medusa production and the polyps resulting from their subitaneous eggs, the population density can grow very rapidly (Werner, 1955).

**DISTRIBUTION:** Southern North Sea and Irish Sea. Helgoland (Hartlaub, 1897; 1899; Werner, 1955); Norfolk coast (Hamond, 1964), Solway Firth (Russell, 1970), Weser, Elbe, and Ems Estuary (Kühl, 1962, 1967; 1971), Belgium (Kramp, 1930; Leloup, 1947). Type locality: Helgoland.

**ADDITIONAL DATA:** The medusae swim very energetically and jerkily. The short marginal tentacles are held out rather stiffly (Hartlaub, 1907).

Hartlaub (1907) observed that the polyps normally do not swim actively and sink slowly to the bottom of the vessel. When sinking, the aboral pole is on top. The polyps are very sensitive to temperature fluctuations. These observations could not entirely be confirmed by Werner (1955), who observed that the polyps do not regularly sink with the oral pole downward, and he thinks that the polyp in the free water does not necessarily orient itself with the aboral pole uppermost.

The aboral stalk rudiment of the polyp has a depression lined with a high epithelium with cylindrical cells, which Hartlaub (1899) considered reminiscent of the pneumatophore of the Physophorae. *Margelopsis haeckelii* has been seen as a model representing an intermediate stage in the evolution of the Siphonophorae (Totton, 1965). This view was contested by Werner (1955), who observed that this organ is used by the hydroid to attach itself temporarily, acting like a sucker organ. The cells of the depression secrete a mucus that is often infested with detritus particles. The aboral stalk rudiment is thus clearly homologous to the corresponding organ by which the tubularian actinula larva attaches itself, and ultimately also the stalk of the mature hydranth.

When the medusa switches from the production of subitaneous- to resting eggs, there may be a period when there are no conspicuous eggs on the manubrium. Such medusae can easily be mistaken for mature males, although they do not have any spermatids (Werner, 1955).

Prévot (1959) depicts a longitudinal section of the polyp. The stalk carrying the medusae buds (blastostyle) is hollow and communicates with the stomach. In the polyp material examined for this study, one bifid oral tentacle was seen.



REMARKS: The original spelling in Hartlaub (1897) is *Margelopsis haeckelii*, which must be retained, despite that Hartlaub (1907) used *haeckeli*, a spelling then used by all subsequent authors (the specific epithet *haeckelii* is the genitive form of the latinized name Haeckelius).

In his study on medusae of Charleston Harbor, McCrady (1859) also described *Nemopsis gibbesii*. His description was mainly based on a series of medusae that are clearly referable to the genus *Nemopsis* (Bougainvilliidae). But McCrady also found a polyp in the plankton which he erroneously associated with this medusa. The polyp closely resembles the polyp of *Margelopsis haeckelii*, only differing in the medusae buds that are dispersed between the two whorls of tentacles. McCrady (1859: figs 4-6) also describes and depicts young medusae stages released by this polyp. As A. Agassiz (1862) and Hartlaub (1899) have already pointed out, McCrady's medusae from the plankton (McCrady, 1859: figs 1-3) were actually *Nemopsis bachei* L. Agassiz, 1849. Therefore, Hartlaub (1899) restricted the name *Margelopsis gibbesii* to the polyp described by McCrady. Although the first revisor was A. Agassiz (1862) who synonymized the name *N. gibbesii* with *N. bachei*, Hartlaub's proposal was followed by Mayer (1910) when he attributed some *Margelopsis* medusae from North Carolina to *M. gibbesii*. McCrady's description did not include mature medusae and the allocation of Mayer appears unfounded, but there is a reasonably good chance that Mayer's identifications were correct, as there are no other *Margelopsis* medusae known from the region.

Thiel (1938) found a *Margelopsis* medusa in the Southern Ocean, which he assigned to *M. gibbesii* and he claimed that *M. gibbesii*, *M. haeckelii* and *M. hartlaubii* are conspecific, a possibility already suggested by Mayer (1910: 80). However, this has not gained acceptance and Kramp (1959) distinguished the medusae of *Margelopsis gibbesii* from *M. haeckelii* by the presence of an apical canal, the thicker jelly and the viviparity in the latter species. The scattered medusae buds in the polyp of *M. gibbesii* can also be added. According to Mayer (1910), *Margelopsis gibbesii* produces male medusae, which indicates that both species differ perhaps also significantly in their life-histories. However, as Werner (1955) cautioned, female medusae that switch from the production of subitaneous- to resting eggs can easily be mistaken for males. More biological details on *M. gibbesii* must be known before both species can be compared and meanwhile it seems appropriate to keep *M. gibbesii* separate from *M. haeckelii*.

Besides *M. haeckelii*, there is also another *Margelopsis* species occurring in the European fauna, namely *M. hartlaubii*. The latter species is known only from the medusa phase occurring in deep waters of Norway, thus contrasting with *M. haeckelii* which is a shallow water species. *Margelopsis hartlaubii* can be distinguished by its lower tentacle number (2-3 per bulb placed beside each other), the thicker jelly, the absence of an apical canal, and the brick-red manubrium.

### *Margelopsis hartlaubii* Browne, 1903

Fig. 14

*Margelopsis hartlaubii* Browne, 1903: 10, pl. 1 fig. 2, pl. 3 fig. 3; Mayer, 1910: 82, fig. 40; Kramp & Damas, 1925: 252, fig. 4; Kramp, 1959: 91, fig. 49; Kramp 1961: 50.

MATERIAL EXAMINED: Zoological Museum Bergen, No 36451, 15 July 1925, Haggernes, Herdla fjord, 200-400 m, 2 medusae, damaged before fixation. – Zoological Museum Bergen, No

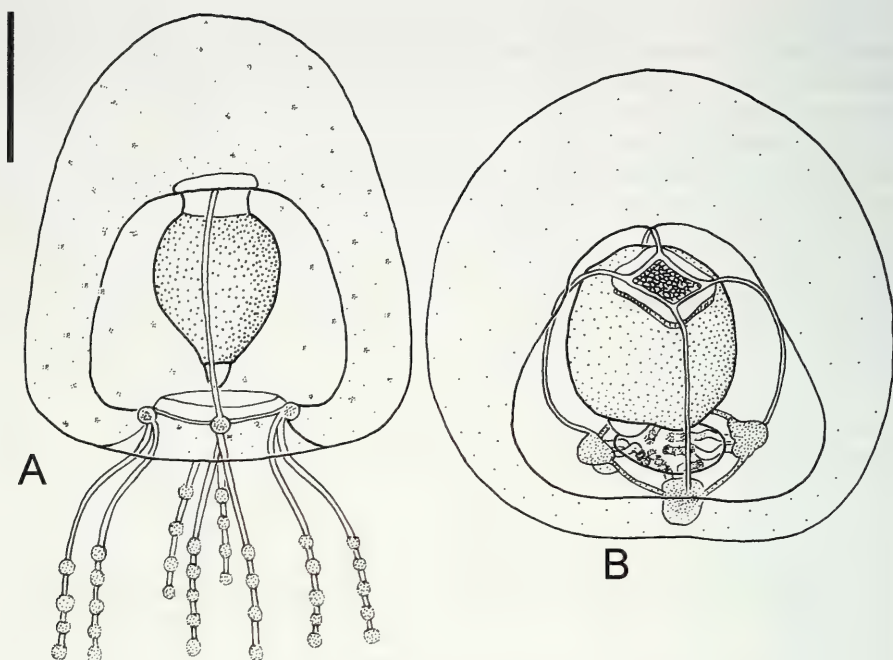


FIG. 14

*Margelopsis hartlaubii* Browne, 1903. A) Redrawn from Browne, scale bar 1 mm (1903). B) Modified after Kramp & Damas (1925).

26825, Herlöfjord, September 1908 (sic), 1 medusa, fertile female, depicted in by Kramp & Damas (1925). – Zoological Museum Bergen, No 26826, ca. 300 m, September 1908, 2 medusae in bad condition, identified by Kramp & Damas (1925).

**DIAGNOSIS:** *Margelopsis* medusa measuring 2-4 mm, umbrella spherical to bell-shaped, jelly relatively thick, no apical canal, with two to three moniliform tentacles per bulb, gonads much bulging, likely no brooding of eggs.

**DESCRIPTION** (after Kramp & Damas, 1925): Polyp stage unknown. Medusa umbrella spherical, 3-4 mm for mature animals, exumbrella with scattered nematocysts. Mesogloea thick, especially at apex, its consistency very soft. The voluminous manubrium takes up a large part of the subumbrellar cavity, its base quadrangular and not covered by gonad; gonad occupies the middle region, shaped like a cube or barrel; oral portion of manubrium conical to cylindrical and mouth margin provided with ring of nematocysts. Four radial canals are narrow and transparent. Four tentacular bulbs thick, triangular, without ocelli, with two or three tentacles with a nematocyst-free base, while the distal region is beaded and end with a terminal knob. Velum broad. Mesogloea and the radial canals perfectly transparent and uncoloured. Stomach, marginal bulbs, and tentacular nematocyst clusters contain a brick-red pigment (observed in living animals).

OWN OBSERVATIONS: Basal, gonad-free region of the manubrium very short; large vacuolated cells could not be seen in the examined preserved material; top of the manubrium is flat, apical canal thus absent; gonad covers most of the manubrium and leaves only short regions uncovered at both ends. Gonad encircles the manubrium without interruption. Tentacle bulbs prominent, their epidermal portion bulging, a gastrodermal chamber present. One sample (26825) mature or almost mature female, numerous eggs are clearly visible within gonad, but no eggs or embryos attached to manubrium as in *M. haeckelii*. Some mature medusae could be mature males. Tentacles distinctly moniliform, apparently quite short, usually two per bulb. Tentacles contain only desmonemes and microbasic mastigophores, stenoteles not observed; small stenoteles seem to be present around mouth opening. Undischarged desmonemes (ca.  $15 \times 10 \mu\text{m}$ ) have a thread with characteristic rope structure. Mastigophores have a spherical capsule of about  $10 \mu\text{m}$  diameter.

BIOLOGY: Occurs in 200-400 m depth, recorded from April to September, but only few records are available.

DISTRIBUTION: Norwegian fjords. No type locality was specified, the original material came from Osterfjord and Herløfjord, 0-400 m.

REMARKS: *Margelopsis hartlaubii* Browne, 1903 is a very rare medusa, known only from a few specimens. Its polyp stage is unknown. The species has been synonymized with *Margelopsis gibbesii* and *M. hartlaubii* by Thiel (1938), a proposal that has not gained acceptance (see remarks under *M. haeckelii*). It is actually quite distinct from *M. haeckelii*: about two times larger, it has a thick mesogloea, it has only two to three tentacles per bulb, and there is no apical canal. Furthermore, the available material suggests that there is no brooding in this species and males may exist.

Nevertheless, more data on this species are needed, e.g. detailed nematocyst data and information on its polyp stage should be obtained in order to confirm the taxonomic position of this species.

#### FAMILY PENNARIIDAE MCCRADY, 1859

SYNONYM: Halocordylidae Stechow, 1921.

DIAGNOSIS: Hydroid colony pinnate, occasionally bushy, stem monosiphonic, giving rise alternately from opposite sides to two series of hydrocladia; hydrocaulus and hydrocladia with terminal hydranths (monopodial); hydranths on short pedicels on upper side of the hydrocladia; hydranths pear-shaped; tentacles of two types: in distal half of hydranth more or less capitate tentacles in one oral whorl and more in indistinct whorls below, on lower part of hydranth one aboral whorl of semifiliform to slightly capitate aboral tentacles; gonophores developing above aboral tentacles, eumedusoids, liberated or not.

Medusa a simple eumedusoid; manubrium not extending beyond umbrella margin; gonads completely surrounding manubrium; four radial canals; four permanently rudimentary tentacles, usually reduced to mere bulbs, without ocelli.

REMARKS: The family contains only the genus *Pennaria* Goldfuss, 1820.



Genus *Pennaria* Goldfuss, 1820

TYPE SPECIES: *Pennaria disticha* Goldfuss, 1820.

SYNONYMS: *Globiceps* Ayres, 1854; *Eucoryne* Leidy, 1855; *Halocordyle* Allman, 1872.

DIAGNOSIS: With the characteristics of the family.

REMARKS: There are several medusa-based species (Kramp 1959, 1968). They are mostly indeterminate and some of them do not belong to the genus *Pennaria* at all (Petersen, 1990). For the synonymy and validity of the name *Pennaria* see Calder (1988) and Gibbons & Ryland (1989). Only *Pennaria disticha* is relevant for the European fauna.

*Pennaria disticha* Goldfuss, 1820

Fig. 15

*Pennaria disticha* Goldfuss, 1820: 89; Mayer, 1910: 24, fig. 1A-E; Brinckmann-Voss, 1970: 40, text-figs 43, 45-50; Gibbons & Ryland, 1989: 387, fig. 5 [taxonomy]; Schuchert, 1996: 142, fig. 85a-c; Watson, 1999: 16, fig. 10A-I; Bouillon *et al.*, 2004: 103, fig. 55A-C.

*Pennaria Cavolinii* Ehrenberg, 1834: 297; Allman, 1872: 364, fig. 80.

*Pennaria cavolini* – Weismann, 1883: 121, pl. 17 figs 1-5, pl. 18.

*Halocordyle disticha* – Rees & Thursfield, 1965: 4; Millard, 1975: 41, figs 16C-G; Hirohito, 1977: 2, fig. 1, pls 1-3; Garcia-Corrales & Aguirre, 1985: 85, figs 1-3 [synonymy]; Morri & Boero, 1986: 31, fig. 11; Wedler & Larson, 1986: 73, fig. 4C; Calder, 1988: 57, figs 43-45 [complete synonymy]; Hirohito, 1988: 28, figs 9a-d, pl. 1 fig. C; Östman *et al.*, 1991: 607, figs 1-18; da Silveira & Migotto, 1991: 437, fig. 1.

MATERIAL EXAMINED: MHNG INVE29809, Mallorca, Cala Murada, coll. P. Schuchert 24 August, 2000 fertile, depth 1 m, 16S sequence AM088481, 18S sequence AY920762. – MHNG INVE 36918, Naples, coll. 1892, few hydranths left. – MHNG INVE 36919, Naples, coll. 1900, fertile. – MHNG INVE 36920, origin unknown, likely Mediterranean, fertile. – MHNG INVE 35468, USA, North Carolina, Morehead City, marine anchorage, fertile, collected 7 October 2000 by Dr Alberto Lindner. – BMNH 1964.8.7.5 *Pennaria tiarella*, slide preparation, Woods Hole, Mass. USA, fertile, hydrocladia bearing a single hydranth, stenoteles max. 25 µm, thus larger than in Weill (1934) and within the range observed for *P. disticha* (Hirohito, 1977). – Honduras, Utila, Blue Bayou Beach, coll. F. Sinniger 13 February 2004, depth 1 m, hydranths more delicate than European forms. – Thailand, Andaman Sea, Koh Phi Phi, Ao Nui, 16 April 2000, 10-20 m, collected by Dr A. Faucci. – New Zealand, Hauraki Gulf, Devonport, 26 July 2002, one medusa from plankton. – See also Schuchert (1996, 2003).

DIAGNOSIS: Feather-like branched hydroid colony (pinnate), firm perisarc, gonophore medusoid, released or not, with four bulbs, no ocelli.

DESCRIPTION: Hydroid colonies forming branching, feather-like shoots, arising from thick creeping, ramified stolons. Growth monopodial with hydranths on all ends. Main axis thick, often curved, monosiphonic, perisarc with smooth stretches and annulated stretches in more or less regular intervals, regularly so distal to insertion of hydrocladia (side-branches) and hydranth pedicels. Hydrocladia of one side form an angle of about 120-140 degrees with those from other side, curved, longest hydrocladia usually found at about 1/3 to 1/2 stem length (measured from base), hydrocladia are about half as thick as stem, they either bear hydranths on pedicels (ramuli) or secondary hydrocladia with hydranths again on pedicels. Pedicels (ramuli) of hydranths originate on upper side of hydrocladia, all approximately of same length and evenly spaced, with annulation at their base or throughout, younger ones without annulation. Hydranths spindle- to pear shaped, hypostome dome-shaped. Tentacles of two types: an aboral whorl of about 12-14 long, filiform to slightly capitate tentacles and



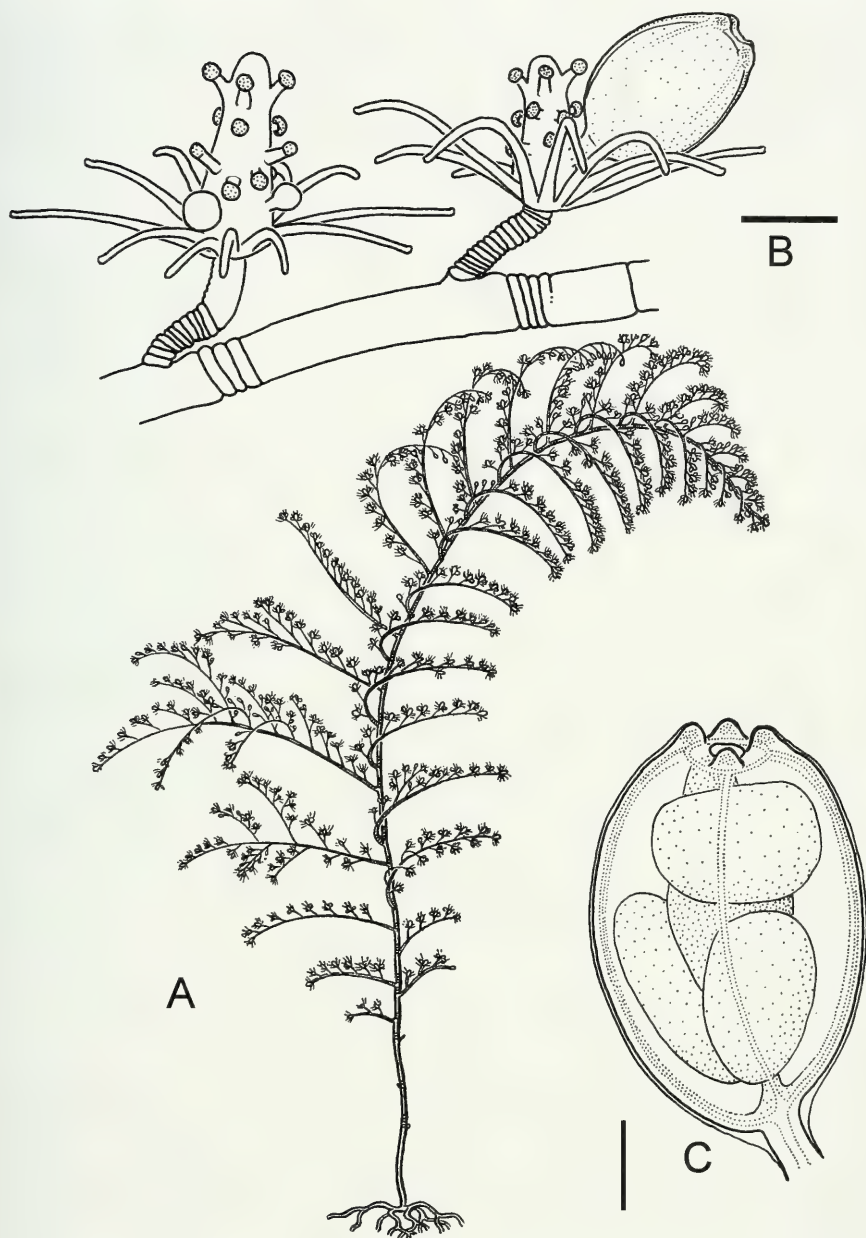


FIG. 15

*Pennaria disticha* Goldfuss, 1820, after Mediterranean material. A) Colony, modified after Mayer (1910), actual size. B) Part of branch with two hydranths, one with an almost mature medusoid, scale bar 0.5 mm. C) Female medusoid that has already spawned some eggs, modified after García-Corrales & Aguirre (1985), scale bar 0.2 mm.

up to 16 short capitate tentacles distributed in two to three indistinct whorls on distal half of hydranth. Knobs of capitate tentacles, except of oral ones, can be reduced to mere nematocyst cap, thus being almost filiform. Nematocysts of aboral tentacles mainly on aboral side and terminally (= semifiliform according to Petersen, 1990), aboral epidermis of filiform tentacles about three times thicker than on oral side, gastrodermal cells chordoid.

Gonophores oblong medusoids arising on short pedicels just above whorl of long filiform tentacles. Gonads encircling manubrium, four radial canals and circular canal present, with four marginal bulbs, with small velum, without ocelli, tentacles normally absent, rarely some rudiments present. Marginal bulbs without a concentration of nematocysts. Colonies gonochoristic, female medusoids with four to six eggs. Gonophores can be released as short-lived medusoids, or they spawn while still attached to hydroid.

Nematocysts of polyp: stenoteles of three to four size classes, microbasic mastigophores with inclusion body, microbasic heteronemes without inclusion body, basitrichous isorhizas, desmonemes. Medusoids with stenoteles only.

Colour of stem dark brown to black, hydrocladia brown, fading distally to clear.

**DIMENSIONS:** Fertile colonies usually around 8-15 cm high, but may exceptionally reach 40 cm. Hydranths 0.9-1.5 mm high; medusoids 0.7-1.1 mm. More measurements are given in García-Corrales & Aguirre (1985). Nematocyst sizes can be found in Millard (1975), Hirohito (1977), García-Corrales & Aguirre (1985), Calder (1988), da Siveira & Migotto (1991), Östmann *et al.* (1991), Schuchert (1996), Watson (1999). Some of these authors also figure them.

**BIOLOGY:** Occurs usually in shallow waters of a few meters depth along rocky coasts with some wave action. In the Mediterranean, the colonies are active from spring to fall, the colonies overwinter as stolons (Brinckmann-Voss, 1970; Morri & Boero, 1986). In more tropical waters they can also be present all year round. Spawning is induced by a reduction of the light intensity (sunset) (Baker, 1936; Brinckmann-Voss, 1970; Calder, 1988; Genzano & Kubota, 2003). The eggs develop in the open water.

Sometimes, the colony form can vary quite drastically, the normal pinnate form can intergrade with a more bushy form (da Silveira & Migotto, 1991). Also Calder (1988) found that the colony form varies depending on wave exposure: colonies from sheltered places were more gracile, internodes of both branches and stem were long and slender, branches and ramuli elongate, while specimens from wave-swept ledges were small and compact, internodes of caulus and branches were thicker and shorter and the branches and ramuli relatively shunted. However, the annulation did not differ significantly.

Prey capture and nematocyst function were investigated by e. g. Clark & Cook (1986); Östman *et al.* (1991), and Kem & Östman (1992). The feeding biology was examined by Pardy *et al.* (1968, as *Pennaria tiarella*).

This species has been the subject of a considerable number of experimental and developmental studies (sometimes under the synonym *Pennaria cavolinii*). Regeneration studies have been made by Cerfontaine (1902), Gast & Godeeski (1903),

Brinckmann-Voss (1970), Tardent (1963, 1965). Hydranth development is described and depicted in Berrill (1952). Gonophore development is documented by Weismann (1883), Berrill (1952), and García-Corrales & Aguirre (1985). Gametogenesis was examined by Weismann (1883). Initially, there are many oogonia in female gonophores, but only a few grow to full size and the others are phagocytosed.

There are many reports on the early development and ultrastructure based on populations from the USA, either named *Halocordyle disticha* or *Pennaria tiarella* (e. g. Hargitt, 1899, 1900, 1904; Cowden 1964, 1965a, 1965b; Summers & Haynes, 1969; Summers, 1970, 1976; Lesh-Laurie, 1976; Thomas *et al.*, 1987; Martin, 1980, 1987, 1988a, 1988b, 1990, 1991, 1992a, 1992b, 2000; Martin & Archer, 1986a, 1986b, 1997; Martin & Thomas, 1977, 1981a, 1981b, 1983; Hotchkiss *et al.*, 1984; Brumwell & Martin, 1996).

**DISTRIBUTION:** Circumglobal in warm temperate to tropical waters. The occurrence at the Azores (Cornelius, 1992) and the Strait of Gibraltar (Medel & López-González, 1996) seem to mark the northern limit for the eastern Atlantic. In the North-Eastern Atlantic also known from the Cape Verde Islands (Rees & Thursfield, 1965), Madeira (Wirtz & Debelius, 2003). Widespread in the western Mediterranean (e. g. Brinckmann-Voss, 1970; García-Corrales & Aguirre, 1985; Bouillon *et al.*, 2004) and eastern Mediterranean (e. g. Vervoort, 1993). Often recorded from the western Atlantic (e. g. Vervoort, 1968; Hirohito, 1977; Wedler & Larson, 1986; Calder, 1988; Migotto, 1996). The distribution further includes the Red Sea (Hirohito, 1977; Vervoort, 1993), Indian Ocean (e. g. Ritchie, 1910; Jarvis, 1922; Stechow, 1925; Mammen, 1963; Millard & Bouillon, 1973; Millard, 1975; Watson, 1999), Malayan Archipelago (Pictet, 1893; Schuchert, 2003), North-Eastern Pacific (Hargitt, 1927; Hirohito, 1977; 1988); south-western Pacific (Schuchert, 1996; Watson, 1999), central Pacific (Cooke, 1977; Gibbons & Ryland, 1989; Kirkendale & Calder, 2003) and western Pacific (Fraser, 1938; 1948; Calder *et al.*, 2003). Type locality: Gulf of Naples, Mediterranean.

**REMARKS:** *Pennaria disticha* is a conspicuous animal and quite well known. For the European fauna, there are no serious taxonomic problems. Its morphological variability was certainly the main reason for its complicated taxonomic history. The complete synonymy is not given here, as this has been done by Calder (1988), Hirohito (1977), García-Corrales & Aguirre (1985), and Gibbons & Ryland (1989).

Most *Pennaria* species based on the hydroid phase were synonymized with *P. disticha*, with the prominent exception of *P. wilsoni* (Hirohito, 1988; Watson, 1999).

*Pennaria tiarella* (Ayres, 1854), a species originally described from Long Island (New York), was already considered to be closely related to *P. disticha* by Mayer (1910). Most subsequent authors (e. g. Fraser, 1944), however, kept it separate. Also Brinckmann-Voss (1970) held it distinct from *P. disticha* on account of the variable length of the ramuli. Later authors (see above) included also *P. tiarella* in the synonymy of *P. disticha*. Weill (1937) reported a comparatively small size for the stenoteles of *P. tiarella*, but an examination of material from the same locality (BMNH 1964.8.7.5, Woods Hole) did not confirm this and the stenoteles have a maximal size that lies within the range found in other populations of *P. disticha* (see Hirohito, 1977).

The embryonic development to the planula larva has been examined in great detail by American students using animals from the USA (identified as *P. tiarella* or *P.*







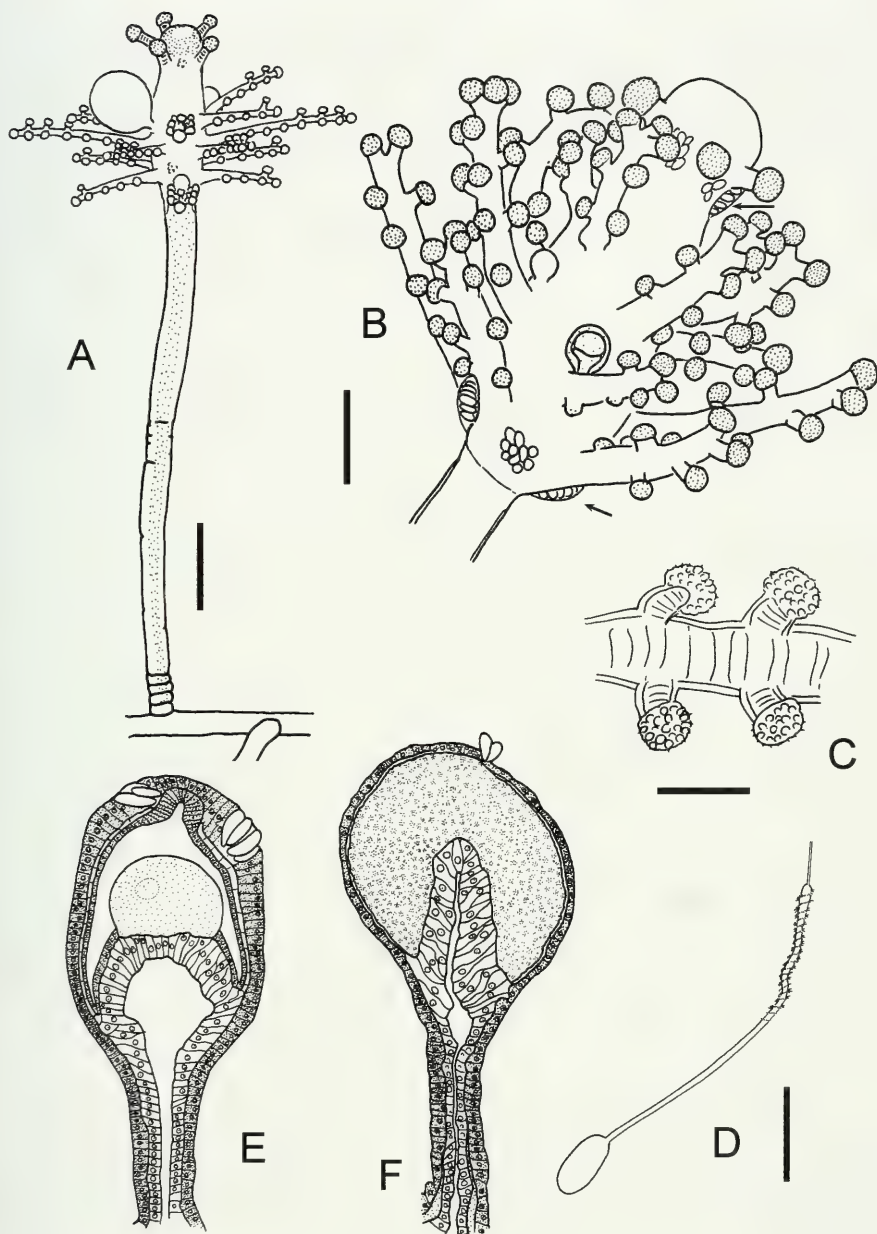


FIG. 16

*Cladocoryne floccosa* Rotch, 1871; A-D after preserved material from the Mediterranean; E-F, after Kühn (1910). A) Hydroid with sporosacs, scale bar 0.5 mm. B) Slightly compressed microscopic preparation of a hydranth, note position of eurytele clusters (arrows), scale bar 0.2 mm. C) Part of tentacles of aboral set, note chordoid gastrodermis, scale bar 0.1 mm. D) Macrobasal eurytele, scale bar 40  $\mu$ m. E) Histological longitudinal section of an almost mature female sporosac. F) Longitudinal section of a mature male sporosac.

*Hydra corynaria* Bosc, 1797.

*Cladocoryne pelagica* Allman, 1876: 255, pl. 10 figs 6-7.

*Polycoryne helleri* Graeffe, 1883a: 202, pl. figs 1-5; Graeffe, 1883b: 320, synonym.

*Cladocoryne simplex* Perrier, 1886: 81, fig. 3.

*Cladocoryne floccosa* var. *sargassensis* Hargitt, 1909: 369, figs 1-2.

*Cladocoryne sargassensis* – Kingsley, 1910: 19, fig. 81.

not *Cladocoryne floccosa* – Rees & Thursfield, 1965: 46 [= *C. haddoni* Kirkpatrick, 1890].

MATERIAL EXAMINED: Cala Murada, Mallorca, Spain, June 1997, on rock in 0.5-2 m depth, fertile, examined alive. – MHNG INVE 29808, Cala Murada, Mallorca, 1 m, 13 August 2000, on *Peysonnellia*, examined alive, infertile. – BMNH 1974.11.21.38, Italy, Naples, 20 April 1967, material of Brinckmann-Voss (1970), not well preserved (maceration by formalin). – MHNG INVE 36913 Naples, Cap Misene 23.01.1895, young sporosacs present, on various substrata. – MHNG INVE 36912, Villefranche-sur-Mer, infertile.

DIAGNOSIS: *Cladocoryne* species with three to four whorls of aboral tentacles, patches of macrobasic euryteles among oral and aboral tentacles, gonophores without radial canals, mature females with one to two eggs.

DESCRIPTION (after own material and literature): Hydroid with unbranched stem or rarely branched once, arising from adhering, ramified stolons. Stems covered by perisarc, smooth or with annulated stretches and becoming thinner distally to terminate below hydranth. Hydranth cylindrical to club-shaped, dome-shaped hypostome; with tentacles of two types in two well-separated sets: a single whorl of four to six short capitate oral tentacles, and 12-22 aboral tentacles in three to four alternating whorls, whorls can be indistinct. Aboral tentacles branched, side-branches short and capitate, in two lateral rows and one median row on upper side; lateral secondary tentacles up to seven per row, median row with zero to two. All side-branches and end of main branch with a terminal spherical nematocyst cluster. Sometimes some secondary tentacles without stalk and reduced to mere nematocyst clusters. Gastrodermis of tentacles chordoid. Hydranth with nematocyst patches or pads on body wall between oral tentacles and lowest aboral tentacles. Colours: hydranth light reddish brown, oral region with conspicuous white pigment.

Gonophores on short pedicels, two to eight borne on the hydranth among or above the upper aboral tentacles, spherical to oblong, remaining fixed as sporosacs without radial canals or circular canal (cryptomedusoid type), females usually with one egg only, colour white.

Nematocysts: stenoteles and macrobasic euryteles.

DIMENSIONS: Colony height a few mm to 12 mm; caulus diameter 0.15 mm; hydranth height 1-1.2 mm, diameter 0.3 mm; length aboral tentacles tentacle 0.7-1.3 mm; sporosac size: 0.3-0.4 mm. Nematocyst sizes are given in Philbert (1936); Weill (1937); Millard & Bouillon (1974); Millard (1975); Migotto (1996); Schuchert (1996); Watson (1999).

BIOLOGY: *Cladocoryne floccosa* has been reported from depths ranging from 0 to 50 m. It has often been observed on *Sargassum* weeds, but also occurs on many other solid substrata like algae, hydroids, sponges, and rocks. In the Mediterranean, it can be found from January to autumn, fertile colonies have been observed in January and from end of April to July (Brinckmann-Voss, 1970; Boero & Fresi, 1986; own observations).

**ADDITIONAL DATA:** Fertile animals often reduce their tentacles, sometimes leading to tentacle-less hydranths (reproductive exhaustion). Kühn (1910) describes the formation of the gonophores and the gametogenesis. The mature female sporosacs usually contain one egg only. Initially there are many eggs, but during the maturation one of them phagocytoses all the others. The embryonic development takes place in the sporosac. Philbert (1936) depicts the metamorphosis of the larva to the primary polyp. The nematocysts are depicted in Weill (1937). A longitudinal section of a hydranth is depicted Prévot (1959) and in Bouillon *et al.* (1987, fertile hydranth). Peña Cantero & García Carrascosa (2002) found branched stems that had up to four hydranths.

**DISTRIBUTION:** Circumglobal in temperate to tropical waters. Along the European coasts known from north-west of Ireland (Allman, 1876, as *C. pelagica*), the English Channel (Rotch, 1871; Philbert, 1936; Teissier, 1965), the Iberian Peninsula (Da Cunha, 1944; Medel & López-González, 1996), western Mediterranean (Du Plessis, 1880; Motz-Kossowska, 1905; Brinckmann-Voss, 1970; Peña Cantero & García Carrascosa, 2002; and more), eastern Mediterranean (Picard, 1958; Morri & Bianchi, 1999). Also known from the western Atlantic (Hargitt, 1909 as *Cladocoryne floccosa* var. *sargassensis*; Migotto, 1996); the Indian Ocean (Millard & Bouillon, 1974; Watson, 1999); the western Pacific (Hirohito, 1988; Schuchert, 1996); the eastern Pacific (Lees, 1968; Calder *et al.*, 2003). Type locality: on stones at low tide at Herm, Guernsey, Channel Islands, United Kingdom.

**REMARKS:** This is a characteristic species that cannot be confounded with any other hydroids of the European fauna. The synonymy is quite well established. *Polycoryne helleri* Graeffe, 1883a was recognized as a synonym by Graeffe (1883b) himself. *Cladocoryne pelagica* Allman, 1876 was described based on a fertile colony found on floating *Sargassum* seaweed northwest of Ireland. Allman kept it distinct on account of its smaller size and the annulated base of the pedicel. These traits are no longer considered diagnostic and in his revision, Philbert (1936) regarded it as a synonym of *C. floccosa*, likewise also *C. simplex* Perrier, 1886, and *C. haddoni* Kirkpatrick, 1890. Most subsequent authors took up Philbert's conclusion, but Bouillon *et al.* (1987) re-described *C. haddoni* based on material from Papua New Guinea and found sufficient differences to *C. floccosa* to permit a reliable identification, even of immature specimens. *Cladocoryne haddoni* was therefore recognized as a distinct species. *Cladocoryne pelagica*, *C. simplex* and *C. sargassensis* are very likely conspecific with *C. floccosa*, although the original descriptions are usually not detailed enough. A re-examination of the type material of *C. pelagica* and a detailed examination of *Cladocoryne* hydroids on *Sargassum* would therefore be helpful. Calder *et al.* (2003) discovered another likely synonym of *C. floccosa*, namely *Hydra corynaria* Bosc, 1797, a *Cladocoryne* species that was also originally described based on material growing on *Sargassum*. Because Bosc's name has not been used since its original description Calder *et al.* (2003), based on provisions of the ICZN, invalidated Bosc's name and to declared *Cladocoryne floccosa* Rotch, 1871 a protected name.

#### FAMILY CLADONEMATIDAE GEGENBAUR, 1856

**SYNONYMS:** Cladonemiden Gegenbaur, 1856; emended to Cladonematidae by Poche (1914: 70); Stauriidae Hincks, 1868; Dendronemidae Haeckel, 1879; Eleutheriidae Stechow, 1923.



REFERENCES: Günther (1903), Hartlaub (1887), Stechow (1923), Bouillon (1985), Calder (1988), Petersen (1990), Bouillon & Boero (2000).

DIAGNOSIS: Hydroid colony stolonal or rarely sparingly branched, arising from creeping stolons. Hydranth spindle-shaped, one whorl of four to ten solid oral capitate tentacles, with or without aboral whorl of filiform tentacles; mouth opening into a pre-oral chamber formed by epidermal gland cells; medusa buds not enclosed in periderm film, carried singly or in clusters at base of hydranth or above filiform tentacles if they are present.

Medusa adapted to benthic mode of life, some species still able to swim freely; with or without a thickened continuous or broken ring of nematocysts around umbrellar margin, with or without brood-chamber above manubrium; manubrium cylindrical, with or without protruding pouches; mouth either simple, or with oral nematocyst clusters, or with ramified oral tentacles; gonads either completely surrounding manubrium, or on manubrial pouches, or in special brood-chamber above manubrium, in latter case also sometimes additionally in subumbrellar epidermis; number of radial canals variable but usually more than four, some may be branched, final number of canals entering circular canal usually corresponding or slightly exceeding the number of marginal tentacles; marginal tentacles hollow, branched, with branches bearing nematocyst clusters and branches having adhesive organs; with abaxial ocelli on tentacle base.

REMARKS: As some Cladonematidae can be cultivated quite easily, they have become the subject of numerous developmental and molecular studies. They thus became quite well known even to non-specialists. The European Cladonematidae species present few taxonomic problems and the species are mostly well known, though the genus *Dendronema* remains problematic. However, taxonomic problems persist at the genus level.

The family Cladonematidae has been kept separate from the Eleutheriidae Stechow, 1923 by a number of authors (for more details see Calder, 1988). The latter family comprised the genera *Staurocladia* and *Eleutheria*. The separation of both families is ambiguous and not necessary and the proposal of Petersen (1990) to unite them is here also adopted. A good example in favour of this is *Staurocladia portmanni* Brinckmann, 1964, which is perfectly intermediate between *Staurocladia* and *Cladonema*, differing basically only in the branching of the tentacles. The genera *Cladonema*, *Staurocladia*, and *Eleutheria* are linked by a number of synapomorphic characters, such as the preoral chamber in the hydroid, the branched medusa tentacles with adhesive ends, and the number of radial canals (Petersen, 1990).

In current usage (Kramp, 1961; Bouillon, 1985; Bouillon & Boero, 2000), the family comprises four genera: *Cladonema*, *Dendronema*, *Staurocladia*, and *Eleutheria*. *Dendronema* is somewhat problematic and the distinction of the three remaining genera relies principally only on the morphology of the capitate tentacles of the medusa. *Cladonema* has tentacles that are branched more than once and its umbrella is not reduced. In *Staurocladia*, the tentacles are only bifid and the upper branch bears additional nematocyst clusters besides the terminal one. *Eleutheria* was diagnosed as having bifid tentacles with a single terminal nematocyst cluster, and additionally a



brood-chamber above the manubrium. There remain, however, problems with this classification, especially so for the scope of *Staurocladia*.

Hartlaub (1917) established the genus *Staurocladia* solely to separate *Eleutheria vallentini*, *E. clapedii*, and others from *Eleutheria dichotoma*. He found this necessary to account for some of the peculiarities of *E. dichotoma*: the brood-chamber, the hermaphroditism, and the gonostyle in the polyp phase. Hartlaub therefore used the combination *Staurocladia clapedii* (Hartlaub, 1889), as this species has no brood-chamber (Müller, 1911; Lengerich, 1923a). Lengerich (1923a) used only a single genus, *Eleutheria*, for all Cladonematidae. Although this would resolve the problem of paraphyletic genera, it creates unwanted name changes for widely known species. Probably unaware of Hartlaub's publication, Gilchrist (1919) had similar thoughts and suggested the genus name *Cnidonema* for the *Eleutheria* species of the southern hemisphere. He also thought that it might be necessary to introduce a new genus for *E. clapedii* if this species should have no brood-chamber. Browne & Kramp (1939) and Kramp (1959, 1961, 1968) took up Hartlaub's diagnosis, but modified the definition so that *Staurocladia* was differentiated from *Eleutheria* by the number of nematocyst clusters per tentacle (*Eleutheria* one, *Staurocladia* more than one) and the absence or presence of a brood-chamber. Browne & Kramp (1939) placed *E. clapedii* in the genus *Eleutheria*, because they were probably unaware that it has no brood-chamber. Brinckmann-Voss (1970) became aware of this discrepancy and changed the genus diagnosis of *Eleutheria* accordingly to "with or without brood-chamber above manubrium". The genera *Staurocladia* and *Eleutheria* were hence distinguished only on account of the number of nematocyst clusters. However, later authors reverted to Kramp's (1961) diagnosis (e. g. Bouillon, 1985; Petersen, 1990; Bouillon & Boero, 2000), but were inconsistent in placing *E. clapedii* in the genus *Eleutheria*.

Distinguishing a genus solely on the number of tentacular nematocyst clusters appears quite ambiguous and very prone to give polyphyletic assemblages. It is thus quite unlikely that the present genera correspond to a monophyletic groups. Unfortunately, there are few useful characters for a phylogenetic analysis of the members of the Cladonematidae. Synapomorphies that can be used to find species groupings are given in table 1. There are more apomorphies, but either they are autapomorphies (gonostyle, very extensible hydranth, brood-chamber, centripetal canals, radial canals with processes, apical cavity), or only examined for one or few species (desmonemes in polyp stage, heteronemes in polyp stage). Some characters are not really usable (lateral or aboral position of nematocyst clusters).

Using these characters for a cladistic analysis of representative members of the family was not very helpful (table 1, figure 17). There are several unresolved polytomies, but it is worth mentioning that *Staurocladia* is evidently a polyphyletic group. In this case, it seems nevertheless prudent not to use these results to redefine the genera because taxonomic stability should be given more value than a classification based on a poorly resolved cladogram. Perhaps a thorough molecular analysis can provide the necessary data, but until then, the diagnoses for *Eleutheria* and *Staurocladia* as given in Brinckmann-Voss (1970) should be used.

TABLE 1  
Characters used in the phylogenetic analysis of the genera of the Cladonematidae

Species / Characters	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Dipirena reesi</i> Vannucci, 1956	1	0	0	0	0	0	0	0	0	0	1	0	0
<i>Dipirena strangulata</i> McCrady, 1859	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cladosarsia minima</i> Bouillon, 1978	?	?	0	0	0	0	0	0	0	1	1	0	0
<i>Cladonema radiatum</i> Dujardin, 1843	1	1	0	1	1	1	1	1	0	1	1	0	0
<i>Dendronema styloendron</i> Haeckel, 1879	?	?	0	1	1	1	1	1	0	1	1	0	0
<i>Eleutheria dichotoma</i> Quatrefages, 1842	1	1	1	1	1	0	0	0	1	0	0	1	1
<i>Eleutheria clapedirii</i> Hartlaub, 1889	0	?	1	1	1	0	0	0	1	0	0	0	1
<i>Staurocladia portmanni</i> Brinckmann, 1964	1	1	0	1	1	1	1	1	0	1	1	0	0
<i>Staurocladia valleritini</i> (Browne, 1902)	1	1	1	1	1	0	0	0	1	0	1	1	1
<i>Staurocladia wellingtoni</i> Schuchert, 1996	0	1	1	1	1	1	1	1	0	0	1	0	0

characters:

- 1 polyp: filiform tentacles: none (0), present (1)
- 2 polyp: gonophore without perisarc film (1)
- 3 mesogloea rigid, medusa thus able to swim freely (0), not so (1)
- 4 medusa tentacles with adhesive ends; absent (0), present (1)
- 5 four radial canals (0), more than four (1)
- 6 radial canals unbranched (0), branched (1)
- 7 oral knobs absent (0), present (1)
- 8 manubrial pouches absent (0), present (1)
- 9 medusae budding absent (0), present (1)
- 10 tentacles branched more than once, no (0), yes (1)
- 11 medusa one terminal nematocyst cluster per tentacle only (0), additional clusters present (1)
- 12 continuous marginal nematocyst ring absent (0), present (1)
- 13 tentacles and radial canals in phase (0), out of phase (1)

note: the character "preoral chamber", likely an apomorphy for the Cladonematidae, was not used, because its state is known for three species only (*C. radiatum*, *S. portmanni*, *E. dichotoma*)

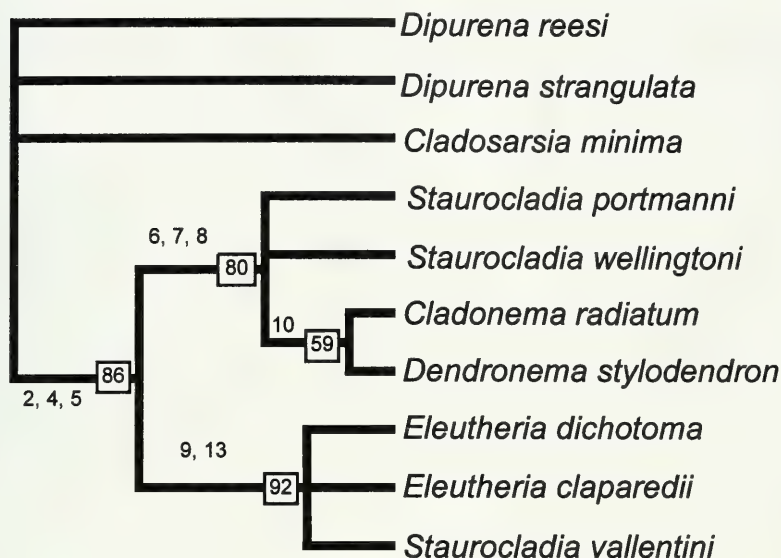


FIG. 17

Genera of the Cladonematidae: Phylogenetic analysis of morphological characters using maximum parsimony: Strict consensus tree of the 17 trees with minimal length (18 steps,  $HI=0.28$ ,  $CI=0.72$ ,  $RI=0.81$ ). The consensus tree of the bootstrap analysis was identical, the percentage of node support is given in boxes. Some selected synapomorphies are also given (numbers along branches, see table 1).

## KEY TO THE CLADONEMATIDAE:

- 1a medusa tentacles branched more than once ..... 2
- 1b medusa tentacles branched once ..... 3
- 2a oral nematocyst knobs of medusa simple ..... *Cladonema*
- 2b oral nematocyst knobs of medusa branched ..... *Dendronema*
- 3a medusa tentacles with a single nematocyst knob ..... *Eleutheria*
- 3b medusa tentacles with a several nematocyst knobs ..... *Staurocladia*

Genus *Cladonema* Dujardin, 1843

TYPE SPECIES: *Cladonema radiatum* Dujardin, 1843 by monotypy.

SYNONYMS: *Stauridia* Forbes, 1848; *Stauridium* Krohn, 1853b.

REFERENCES: Kramp (1961); Bouillon (1985); Calder (1988); Petersen (1990); Bouillon & Boero (2000).

DIAGNOSIS: Hydroid mostly stolonial, occasionally branched, one oral whorl of four to five capitate tentacles, with or without filiform tentacles, medusa buds borne singly on hydranth body immediately above filiform tentacles or in similar position when these are absent. Medusae adapted for swimming and adhering to surfaces, with bell-shaped umbrella; manubrium cylindrical, in adults with pouches, gonads without perradial separations, mouth short, unbranched lips bearing four to six spherical nematocyst clusters; without apical chamber above manubrium; radial canals bifurcated or simple, final number of canals entering circular canal usually of same number

as marginal tentacles; marginal tentacles branching, each with one to six proximal branches ending in an adhesive organ and one to ten more distal branches with nematocyst clusters; abaxial ocelli with lens.

***Cladonema radiatum* Dujardin, 1843**

Fig. 18

*Cladonema radiatum* Dujardin, 1843: 1134; Dujardin, 1845: 271, pl. 14 figs C1-C7, pl. 15 figs C8-C19; Krohn, 1853b: 420, pl. 13; Keferstein & Ehlers, 1861: 85, pl. 13 fig. 5; Van Beneden, 1867: 139, pl. 12; Hincks, 1868: 62, text fig. 5, pl. 11; Allman, 1871-1872: 216, pl. 17; Hincks, 1872: 391, pl. 21, fig. 6; Hartlaub, 1887: 266, 651; Billard, 1905: 500; Hartlaub, 1907: 132, figs 123-126; Müller, 1908: 30, pl. 3 figs 1-2; Mayer, 1910: 99, figs 53-55; Lengerich, 1923a: 331, figs A-S; Weill, 1937: 443, fig. 1; Russell, 1953: 105, figs 49-51; Kramp, 1959: 96, fig. 55; Brinckmann & Petersen, 1960: 388, fig. 2; Kramp, 1961: 57; Kramp, 1968: 22, fig. 52; Naumov, 1969: 245, figs 113, 117A-H; Brinckmann-Voss, 1970: 76, figs 88-89, pl. 5 figs 1-2; Bouillon, 1971: 333, figs 4.5-7; Millard & Bouillon, 1973: 12, fig. 1A; Rees, 1979: 300; Calder, 1988: 67, fig. 50; Hirohito, 1988: 41, fig. 12a-b; Schuchert, 1996: 131, fig. 80a-d; Migotto, 1996: 23, fig. 4e-g; Bouillon *et al.*, 2004: 88, fig. 48B-D.

*Coryne stauridia* Gosse, 1853d: 257, pl. 16 figs 1-5.

*Syncoryne stauridia* Krohn, 1853a: 137.

*Cladonema Gegenbauri* Haeckel, 1879: 109.

*Cladonema Krohnii* Haeckel, 1879: 109.

*Cladonema Dujardinii* Haeckel, 1879: 109.

*Cladonema Allmani* Haeckel, 1879: 109.

*Stauridium cladonema* Haeckel, 1879: 109.

*Cladonema perkinsii* Mayer, 1904: 18, pl. 4 fig. 35; Mayer, 1910: 101, pl. 9 fig. 1.

*Cladonema mayeri* Perkins, 1906: 118; Mayer, 1910: 101, pl. 9 figs 2-3.

*Stauridia radiatum* – Mayer, 1910: 100.

*Eleutheria radiata* – Lengerich, 1922: 210, fig. 1; Lengerich, 1923a: 313, figs G-S.

? *Cladonema novae-zelandiae* Ralph, 1953: 72, fig. 20.

**MATERIAL:** Aquarium culture of polyp stage originating from the Mediterranean, 18 January 1991, life-cycle observed to mature medusa. – MHNG INVE 29909, Roscoff, Brittany, polyps on holdfast of laminarian, collected 1 June 2001, cultured at room temperature, medusae buds developed, very cold-sensitive, died at <14°, grew well at 22-30°C; 16 S sequence accession number AY512539. – Three medusae, Bay of Portoferraio, Island of Elba, Italy, collected July 2005 by dragging a plankton net over a *Posidonia* meadow, depth 2-4 m; colour of whole medusa light brown, 16 S sequence accession numbers of two different individuals AM088482 and AM088483. – MHNG INVE 37640, 19 February 2004, polyps on "living stones" from tropical aquarium, origin unknown, medusae cultivated to near maturity, 16 S sequence accession number AM088484, appeared identical to other *C. radiatum* medusae except that proximal parts of radial canals were white, also on manubrium longitudinal stripes of white pigment; this material belongs thus perhaps to a separate species of tropical origin, a fact also suggested by the deviating 16S sequence.

**DIAGNOSIS:** Hydroid with one oral whorl of capitate tentacles, each with up to ten gastrodermal cells, with one aboral whorl with usually four filiform tentacles. Medusa tentacles branched several times, two and more adhesive branches in fully mature animals, two and more capitate branches; manubrium shorter than bell cavity, mouth with four to five spherical nematocyst clusters, gonads on manubrial pouches and on manubrium, radial canals bifurcated or not.

**DESCRIPTION:** Hydroid colonies stolonal or rarely branched, arising from creeping, ramified stolons, hydranths on pedicel of variable length, but usually longer than hydranth. Perisarc smooth, terminating shortly below filiform tentacles.



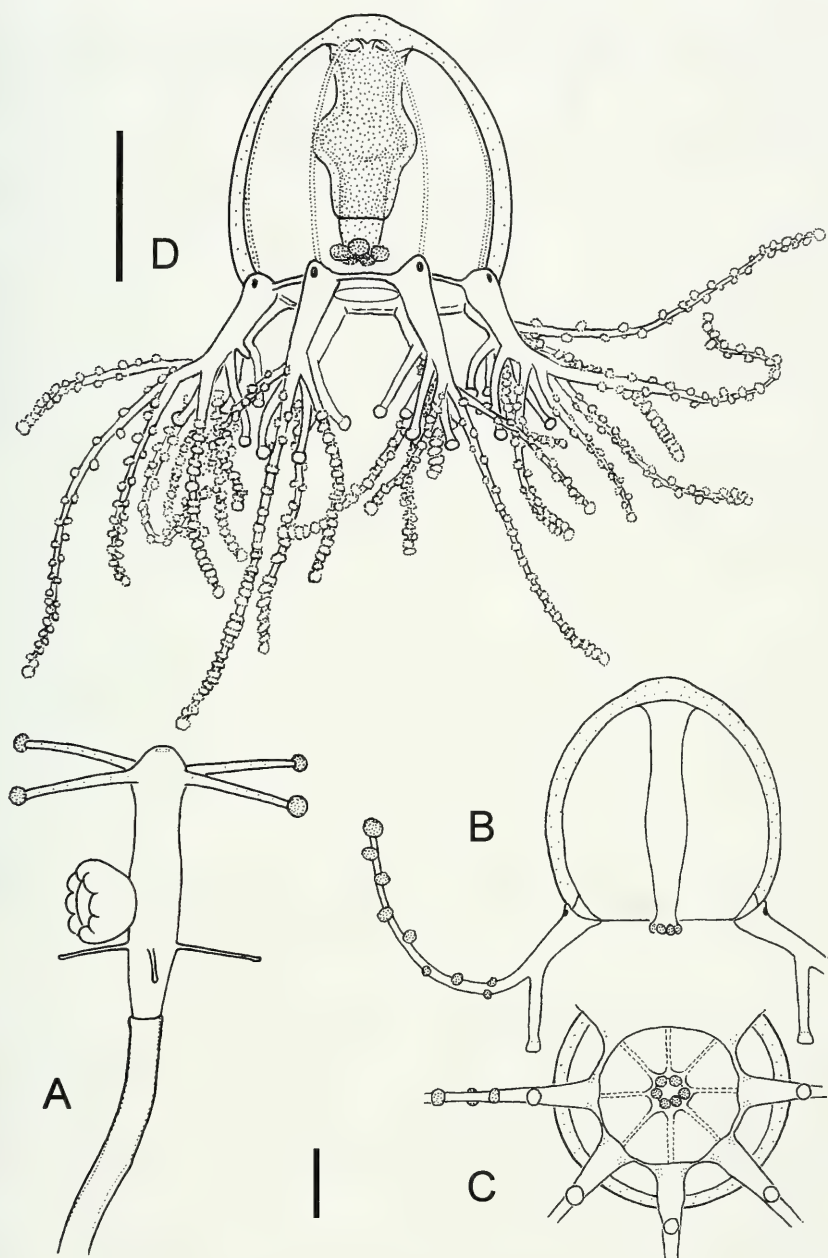


FIG. 18

*Cladonema radiatum* Dujardin, 1843. A-C, after living material from Brittany; D, after photos of living Mediterranean medusae. A) Polyp with medusa bud, scale bar 0.2 mm. B) Lateral view of newly released medusa in optical section, same scale as A. C) Oral view of newly released medusa. D) Mature male medusa, scale bar ca. 1 mm.

Hydranths with one oral whorl of four to five capitate tentacles, each tentacle with seven to ten chordoid gastrodermal cells. Below capitate tentacles one whorl of four (occasionally five) slender, filiform tentacles with a slight terminal swelling, without nematocysts. Hypostome with an epidermal preoral chamber. Medusae buds naked, arising above filiform tentacles. Nematocysts: stenoteles and mastigophores.

Newly released medusa with eight to ten bifid tentacles, upper branch with a terminal nematocyst cluster and a few oral-aboral clusters (Fig. 18).

Adult medusa with bell-shaped umbrella, slightly higher than wide, jelly moderately thin, sometimes with a slight apical projection, velum rather broad. Medusa able to swim freely but mostly remains attached, does not move by crawling. Manubrium spindle-shaped, shorter than or as long as bell cavity, with five (sometimes four or six) perradial pouch-like protuberances in its middle region, protuberances rather shallow, size variable. The gonads completely surround the upper two thirds of manubrium inclusive the pouches. Mouth with four to five bulbous nematocyst clusters. Radial canals may bifurcate close to the manubrium and eight to ten canals reach the circular canal, branching pattern variable even in individuals from the same colony. Number of marginal tentacles corresponds to the number of radial canals. Each tentacle base with an abaxial ocellus. Marginal tentacles branched, with elongated thickened base and a long main branch from the underside of which grow one to six short tentacles acting as adhesive organs, the ends of the adhesive tentacles have a distinct spherical swelling at their end; distal to the adhesive branches the main branch gives off up to five side-branches bearing nematocyst clusters alternating in aboral and oral position and one larger terminal cluster, proximal side-branches originate orally, more distal ones issuing laterally from the main branch. Colour of stomach and marginal tentacles red, bright-red or brown; ocelli black or deep crimson. Nematocysts: stenoteles, desmonemes.

**DIMENSIONS:** Hydroid colonies up to 25 mm, hydranth about 1 mm; newly released medusa 0.7-1.0 mm, adult medusa up to 3 mm high. Nematocysts see Weill (1936), Brinckmann & Petersen (1960), Schuchert (1996).

**BIOLOGY:** For Mediterranean populations, Brinckmann-Voss (1970) reports that the polyp colonies remain small in nature (2-3 hydranths), they were found in shaded places on algae and other hard substrata. From end of June to the end of July, the medusae were caught in large numbers in *Posidonia* beds, later they are rare or absent. The development of the medusae-buds is quick, at 18°C it takes only 6-7 days until the medusa is set free. Also Motz-Kossowska (1905) observed the medusae only from June to August, rarely also in October.

**ADDITIONAL DATA:** The polyps of *Cladonema radiatum* are easy to keep in laboratory. Dujardin (1843) kept them for several years, Lengerich (1923a) reports a colony that was kept for more than 30 years in an aquarium in Berlin. Also the medusa is relatively easy to keep and reaches maturity in culture vessels. It also turns up regularly in aquariums. It is thus an ideal experimental organism and therefore there is a large number of developmental and histological investigations which cannot be reviewed here in detail.

The morphology, histology, and ultrastructure was dealt with in detail by e. g. Müller (1908); Lengerich (1923a; 1923b), Brien (1942), Bouillon (1968), Bouillon & Houvenaghel (1970), Tardent & Stössel (1971), Weber & Tardent (1978), Weber (1980, 1981a, 1981b), Bouillon *et al.* (1988), Falugi *et al.* (1994).

The nematocysts and their biology were investigated by: Weill (1936), Brien (1942), Achermann & Tardent (1973), and Bouillon (1971).

The development and medusae budding was investigated by e. g.: Pasteels (1939, 1941), Brien (1941, 1942), and Bodo (1970).

The behaviour of the medusa is described by: Allman (1872), Browne (1900), Billard (1905), Lengerich (1923a), and Russell (1953, summary). It is important to note in this context that the medusa does not crawl like *Eleutheria dichotoma*, but changes place by swimming. The adhesive tentacles are thus only used for clinging to a surface. There is also a differences in the ultrastructure of the adhesive tentacles (Bouillon, 1968).

The medusae can be hermaphroditic, but usually this is rare (Hartlaub, 1887; Müller, 1908; Bouillon & Houvenaghel, 1970). Bouillon & Houvenaghel (1970) found only two hermaphroditic animals among fifty medusae, while others observed none (Lengerich, 1923a). They can be successive hermaphrodites beginning either as females or males (Hartlaub, 1887).

**DISTRIBUTION:** North-Eastern Atlantic: Norway (Christiansen, 1972), Great Britain and Ireland (Hincks, 1868; Allman, 1872; Russell, 1953), Sweden (Segerstedt, 1889; Aurivillius, 1898; Kramp, 1935); Denmark (Kramp, 1935); Helgoland (Richters, 1908); Holland (Vervoort, 1946), Belgium (Leloup, 1947), Atlantic coast of France (Dujardin, 1843; Billard, 1905; Teissier, 1965), Atlantic coast of the Iberian Peninsula (Medel & López-González, 1996). Mediterranean (numerous records, e. g. Brinckmann-Voss (1970), Boero & Fresi (1986), Daly Yahia *et al.* (2003, Tunisia), Bouillon *et al.* (2004)). Present in the Black Sea (Thiel, 1935). Also known from Brazil (Migotto, 1996), Bermuda (Calder, 1988), Indian Ocean (Millard & Bouillon, 1973), ? New Zealand (Schuchert, 1996), Japan (Hirohito, 1988; introduced?). Type localities: Dujardin (1843) described material from the Mediterranean, St. Malo, and Lorient (France).

**REMARKS:** The medusa of *Cladonema radiatum* is quite variable with respect to the number and branching patterns of the radial canals. Also the number of adhesive tentacles, manubrial pouches, and oral nematocyst clusters is variable in natural populations. Even monoclonal animals show some degree of variation.

Weill (1937) examined 106 specimens collected at Bermuda and these encompassed the characteristics of *C. radiatum*, *C. perkensii*, and *C. mayeri*. Weill concludes that the three nominal species were no more than varieties of one rather variable species, as Mayer (1910) had suggested earlier. This view has been adopted by most subsequent authors (e. g. Russell, 1953; Kramp, 1959; Kramp, 1961).

There are several nominal *Cladonema* species known, but sometimes the differences to *C. radiatum* are unclear or minimal (Kramp, 1968). Rees (1979) and Stepanjants *et al.* (1993) review all the differences between the different nominal species. Stepanjants *et al.* (1993) concluded that there were only two valid species, namely *C. radiatum* and *C. californicum*.



The medusae of *Cladonema californicum* Hyman, 1947 was held distinct from all other described *Cladonema* in having only one adhesive tentacle branch and one to two nematocyst bearing branches, and a manubrium that protrudes from the velar opening (Hyman, 1957; Rees, 1979). According to Hyman (1957), the gonads cover the manubrium on the pouches and the rest of the manubrium, this in contrast to the diagnosis in Kramp (1968). The polyp appears indistinguishable from *C. radiatum*.

The polyps of the Californian *Cladonema myersi* Rees, 1949 lack filiform tentacles, the medusa lacks branching radial canals, and the gonad covers the entire manubrium (Naumov, 1969). Likewise, the polyps of the Japanese *Cladonema uchidai* Hirai, 1958 also lack filiform tentacles.

Naumov (1955) described *Cladonema pacificum*, which he later (1960, 1969) synonymized with *C. myersi*. This was contested by Hirohito (1988). Rees (1979) and Hirohito (1988) think that *C. uchidai* belongs to *Cladonema pacificum*. This species is distinguished from *C. radiatum* by a gonad that covers almost the whole manubrium, and not only the upper 2/3 (compare Bouillon *et al.*, 1988: fig. 1).

*Cladonema novaezelandiae* Ralph, 1953 has been synonymized with *C. radiatum* by Schuchert (1996). However the polyp stage of the New Zealandic *Cladonema* remains unknown and it may turn out to be different from *C. radiatum*. Its synonymy with *C. radiatum* is therefore not sufficiently established.

Although it is evident that many nominal *Cladonema* species are currently not objectively distinguishable, it is still likely that several distinct biological species have been included in *C. radiatum*. The 16S sequences of the *Cladonema* sample found in aquarium with tropical material (see above in material examined) differs in more than 25% of its positions from the Atlantic and Mediterranean sequences. Such a difference represents more likely interspecific variation (comp. Schuchert, 2005). The differences among the examined European sequences are less than 4%.

The hydroid of *Cladonema radiatum* is rather difficult to distinguish from hydroids of some Corynidae (Schuchert, 2001b). Brinckmann & Petersen (1960) found that the number of gastrodermal cells in the capitate tentacles offers a reliable tool to discriminate *Cladonema radiatum* and *D. reesi*: while *C. radiatum* has 10 or less cells, *D. reesi* has 13-18 (see also Schuchert, 2001b). Additionally, the macrobasic heteroneme is characteristic for *Cladonema radiatum*. Also the hydroid of *Staurocladia portmanni* is very similar. Brinckmann-Voss (1970) found that *S. portmanni* polyps have regularly six filiform tentacles, while *C. radiatum* has usually four, sometimes five.

### Genus *Eleutheria* Quatrefages, 1842

TYPE SPECIES: *Eleutheria dichotoma* Quatrefages, 1842, by monotypy.

SYNONYMS: *Clavatella* Hincks, 1861; *Herpusa* Schmidt, 1869.

REFERENCES: Kramp (1961); Bouillon (1985); Petersen (1990); Bouillon & Boero (2000).

DIAGNOSIS: Hydroid with an oral whorl of up to ten capitate tentacles, without aboral filiform tentacles; medusae buds carried in clusters on short blastostyles (gonostyle) or singly at base of hydranth. Medusae adapted for crawling, unable to swim; umbrella with or without continuous ring of nematocysts along margin; with four or



more simple and short radial canals; manubrium with broad base, conical, with simple circular mouth; with or without brood-chamber above base of stomach; gonads either on manubrium, or in brood-chamber from where they can also extend to the epidermis of the subumbrella; 6-14 bifurcated marginal tentacles, one upper branch with a single terminal nematocyst knob, one lower branch with adhesive organ; asexual reproduction through medusa budding present.

REMARKS: The problems concerning the distinction of *Eleutheria* and *Staurocladia* have been discussed above under remarks at the family level.

KEY TO THE EUROPEAN *ELEUTHERIA* MEDUSAE:

- 1a medusa buds on outside, with brood-chamber . . . . . *Eleutheria dichotoma*  
 1b medusa buds in subumbrella, no brood-chamber . . . . . *Eleutheria clapedii*

***Eleutheria dichotoma* Quatrefages, 1842**

Figs 19A-C, 20

*Eleutheria dichotoma* Quatrefages, 1842a: 270, pl. 8; Quatrefages, 1842b: 168; de Filippi, 1866: 375, pl. 1; Hartlaub, 1886: 706, text. fig.; Hartlaub, 1907: 127, figs 119-120; Mayer, 1910: 94, figs 46-48; Müller, 1908: 34, pl. 3 figs 3-7, pl. 4; Lengerich, 1923a: 359, figs R'-Z', D2; Drzewina & Bohn, 1913: 49, figs 26-37; Weill, 1936: 816; Russell, 1953: 110, figs 52-53; Kramp, 1961: 59; Naumov, 1969: 249, figs 118-121; Brinckmann-Voss, 1970: 79, figs 90-92; Bouillon, 1994: 146, fig. 55; Bouillon, *et al.* 2004: 88, fig. 48B-D.  
*Clavatella prolifera* Hincks, 1861: 73, pls 7-8; Hincks, 1868: 73, pl. 12 fig. 2; Allman, 1872: 384, pl. 18.

*Herpusa ulvae* O. Schmidt, 1869: 993, fig.

*Eleutheria tetranema* Haeckel, 1879: 106.

*Eleutheria pentanema* Haeckel, 1879: 106.

*Eleutheria hexanema* Haeckel, 1879: 106.

*Eleutheria anisonema* Haeckel, 1879: 106.

*Eleutheria heptanema* Haeckel, 1879: 107.

*Eleutheria octonema* Haeckel, 1879: 107.

*Eleutheria dichocnida* Haeckel, 1879: 107.

*Eleutheria cnidobdella* Haeckel, 1879: 107.

*Eleutheria dichobdella* Haeckel, 1879: 107.

*Eleutheria heteroclada* Haeckel, 1879: 107.

*Cladonema prolifera* – Motz-Kossowska, 1905: 47.

*Eleutheria krohni* Krumbach, 1907: 453.

*Eleutheria gemmipara* Du Plessis, 1909: 376.

not *Eleutheria dichotoma* – Claparède, 1863: 4, pl. 1 figs 4-10 [= *E. clapedii*].

not *Eleutheria dichotoma* – Spagnolini, 1876: 312 [= *E. clapedii*].

MATERIAL: MHNG INVE 34228, Mediterranean, Banyuls-sur-Mer, île Grosse, 2 May 2002, 0 m, > 10 medusae on *Ulva lactuca*, with eggs/planulae in brood-chamber, examined alive, development to primary polyp followed, DNA sample deposited, 16S sequence accession number AM088485. – MHNG INVE36841 living polyp colony obtained from B. Schierwater, collected 1995, Spain, Tossa de Mar, La Fosca, medusae buds developed after a few days of cultivation.

DIAGNOSIS: *Eleutheria* medusa with brood-chamber, medusae buds outside on bell rim or exumbrella, normally six tentacles, tentacles bifurcated once in middle, trunk and branches of about the same length, often hermaphroditic, nettle ring thick.

DESCRIPTION: Hydroid stolonial, stolons creeping, branched, perisarc smooth; hydranths with very short pedicels, sometimes almost sessile, pedicel covered by thin periderm, sometimes widened like a funnel. Hydranth body cylindrical, very extensile, fully extended with very thin body and swollen terminal region, one oral whorl of four

to eight capitate tentacles, 16-18 gastrodermal cells per tentacle. Filiform tentacles absent. Medusae buds in lowest part of hydranth, either singly or in clusters borne on short gonostyle (tubular outgrowth of body wall, up to four per hydranth), gonostyles branching or not, carrying up to four medusae buds, buds not protected by periderm covering. Preoral cavity visible in living animals. Colour: gastrodermis white or pink, depending on food.

Medusa umbrella somewhat flattened-hemispherical, with its oral surface more or less six-sided and with well-developed thickened marginal ring packed with nematocysts. Velum broad, usually closing umbrella and opened only when feeding. Manubrium broadly conical, filling almost the entire subumbrella, extensible beyond umbrella, mouth simple and without nematocyst knobs. Gonads in specialized cavity or brood-chamber situated above the manubrium, often male and female gametes present, female gonads in lower epithelium of brood-chamber, male gonads in upper epithelium, and also on subumbrella, embryos develop in brood-chamber, up to seven planulae can be present. Radial canals very short, usually six in number. Ring canal relatively large, widening at junctions with radial canals. Tentacles hollow proximally, chordoid distally, mostly six or five present, but rarely also other numbers possible, bifurcated at about middle, upper branch only with one terminal nematocyst cluster, lower branch terminating in adhesive organ used to cling to the substratum. One abaxial ocellus on base of each tentacle. Medusae budding from bell margin and lower part of exumbrella regularly present, also in reproductive animals. Colours: body olive-cream, ocelli red to brown. Nematocysts: polyp with stenoteles of two size classes; medusa with stenoteles and desmonemes.

**DIMENSIONS:** Polyp 1-6 mm and more, very contractile; tentacular capitula diameter 0.25-0.30 mm. Medusa bell diameter 0.4-0.8 mm, tentacle length 1.8 mm. Egg size 47-93  $\mu\text{m}$  (Tardent, 1978). Stenoteles of polyp: (30-33.5)x(19-21) $\mu\text{m}$  and (16.5-18.5)x(9-11) $\mu\text{m}$ . Stenoteles of medusa: (12-24)x(7-16) $\mu\text{m}$ , apparently not falling into distinct, different size classes. Desmonemes of medusa: (7.5-9.5)x(4-5) $\mu\text{m}$ .

**DISTRIBUTION:** Present along all coasts of Europe and the Mediterranean, rarer in the southern North Sea, perhaps absent in the Baltic Sea. Also known from the Black Sea (Thiel, 1935), Madeira (Friedrich, 1961), and the Caribbean (Spracklin, 1982). The northernmost occurrence seems to be near Bergen in Norway (Kramp & Damas, 1925). Records for the Swedish west coast are given by Hartlaub (1886), for the British Isles by e. g. Hincks (1861, 1868), Allman (1872), for France by e. g. Drzewina & Bohn (1913) and Teissier (1965), for the Atlantic coast of Spain by Medel & López-González (1996). The Mediterranean records are summarized in Brinckmann-Voss (1970). Type locality: Chausey Isles, English Channel.

**BIOLOGY:** The polyp has only rarely been found in nature. Hincks (1868) observed that in England medusae budding takes place during summer and autumn. The medusa lives attached to various seaweeds, preferably on *Ulva* species, but also on *Cystoseira*, *Gelidium* and other substrata. It lives in shallow depths, also frequently in tide pools. Brinckmann-Voss (1970) found the medusa also in deeper waters (20 m). Sexual reproduction in the English Channel was observed in May to June and October to November (Teissier, 1965).

ADDITIONAL DATA: *Eleutheria dichotoma* is easy to keep in small containers and it has therefore been a favourite subject for a number of studies. Hartlaub (1886) examined the formation of the brood-chamber in histological sections. The subumbrellar epidermis forms canal-shaped cavities that penetrate the region above the stomach. The fusion of these canals in the centre then creates the brood-chamber. The brood-chamber is connected to the subumbrella by interradian openings (thus usually six). The gastrodermis of the manubrium becomes completely separated from the umbrella. The eggs mature in the lower epithelium of the chamber, while spermatids develop in the upper epithelium. However, only 12% of Hartlaub's animals were hermaphroditic, the others were all female. Müller (1908) supplemented the former observations with more details. He found that the brood-chamber develops very early in development, even while the medusa is still attached. The fraction of hermaphroditic animals he found was higher, namely 35% of the fertile animals. Müller (1908) also reported that the spermatogonia can also be produced in small patches of the subumbrellar epidermis. Krumbach (1907) made many observations on the living animal and he describes its movements. He found that the velum tightly closes the umbrella. This he considered might reduce desiccation in case the animal is exposed to the air. Drzewina & Bohn (1913) studied the variability of the tentacle numbers in animals collected from nature. They found the following distribution among 39 animals: 1x8 tentacles, 1x7 tentacles, 30x6 tentacles, 7x5 tentacles. They also made regeneration experiments, observed anomalies, and investigated the influence of cyanide. The budding of medusae from the medusa bell includes also part of the radial canal, thus the medusa buds are of ento- and ectodermal origin (Hartlaub, 1886; Lengerich, 1923b). The development of the medusa bud includes also the formation of an entocodon. The development of the gametes takes place in the brood-chamber and the planulae are released by a rupture of the umbrella. The latter heals again after the release (Lengerich, 1923a). The histology of the medusa has been examined by several authors, e. g. Hartlaub (1886), Lengerich (1923a), Bouillon (1968), van de Vyver & Bouillon (1969), and Bouillon (1994: fig. 55). Bouillon (1968) also examined the histochemistry and ultrastructure of the adhesive organs. The haploid chromosome number is 6 (Makino, 1951; cited in Tardent, 1978). Hauenschild (1956) observed that the ability to produce gametes can irreversibly be lost in some clones, this either naturally or induced artificially. Hadrys *et al.* (1990) examined the feeding behaviour of the medusa. Ender (1997) analyzed the population structure using mitochondrial DNA sequences. Further experimental, developmental and structural details are given by Weill (1936), Hauenschild (1957a, b), Weiler-Stolt (1960), Schierwater (1989), Schierwater & Havenschild (1990), Schierwater *et al.* (1991, 1992), Kuhn *et al.* (1996), Schierwater & Hadrys (1998).

REMARKS: The synonymy is given by Bedot (1912, 1916, 1918), Mayer (1910), Lengerich (1923a), Kramp (1961), and Russell (1953). In its medusa phase, *Eleutheria dichotoma* is very characteristic and among the European medusae it can only be confounded with *E. clapedii*. The external medusae buds and the tentacles that are bifurcating in the middle make *E. dichotoma* immediately recognizable. In addition, *E. dichotoma* has usually five to six tentacles, while most *E. clapedii* have eight. Their polyps appear very similar and are perhaps not distinguishable.



***Eleutheria clapedii* Hartlaub, 1889**

Figs 19D &amp; 21

*Eleutheria dichotoma* – Claparède, 1863: 4, pl. 1 figs 4-10; Spagnolini, 1876: 312.[not *Eleutheria dichotoma* Quatrefages, 1842].*Eleutheria heteronema* Haeckel, 1879: 106.*Eleutheria diplonema* Haeckel, 1879: 106.*Eleutheria clapedii* Hartlaub, 1889: 665; Mayer, 1910: 95, fig. 49; Brinckmann-Voss, 1970: 80, figs 93-95.*Eleutheria clapedei* – Hartlaub, 1907: 129, fig. 128; Müller, 1911: 159, pl. 3 fig. 1; Drzewina & Bohn, 1913: 49, figs 26-37; Lengerich, 1922: 211, fig. 2; Lengerich, 1923a: 336, figs V-Z, A1-F1; Browne & Kramp, 1939: 274; Kramp, 1961: 59; Bouillon *et al.*, 2004: 88, fig. 48E-F.*Staurocladia clapedei* – Hartlaub, 1917: 401.

**MATERIAL:** Roscoff, France, September 2004, one medusa in plankton, mature male with medusae buds; one immature medusa with medusae buds on *Cystoseira* spec., developed eggs after 6 weeks of cultivation. 16S sequence of male medusa accession number AM088486.

**DIAGNOSIS:** *Eleutheria* medusa without brood-chamber, medusae buds within subumbrella, usually eight tentacles, tentacles bifurcated once in distal region and trunk thus clearly longer than branches, gonochoristic, nettle ring not conspicuous.

**DESCRIPTION:** Sedentary medusa clinging to seaweeds, flat, umbrella slightly shallower than a hemisphere, without jelly, usually eight to nine tentacles (range 5-10), not in phase with radial canals, tentacles relatively long when expanded, held horizontal, bifurcated at 1/4 to 1/6 from end, the two branches of equal length, upper branch ending in a capitulum, capitulum flat-button-shaped to oval, lower tentacle branch ends in adhesive pad, not much enlarged, used to cling to the substrate. One abaxial ocellus at base of each tentacle, colour red. Stomach large, filling nearly entire subumbrella, conical; four to six short radial canals; ring canal thick, underlying nettle ring inconspicuous but present. Velum conical, broad, usually closed and usually only opened for feeding, releasing medusae, gametes or excrements. Gonochoristic, gonads develop in stomach epidermis, without brood-chamber but embryos develop within subumbrella. Asexual multiplication by medusae budding frequent, buds arise from epidermis over radial canal in the subumbrellar cavity. Budding usually stops when gonads develop. Colours: Manubrium and medusae buds orange, rest whitish-cream or transparent. Nematocysts: stenoteles and desmonemes.

Polyp only known from cultivation experiments, colonies stolonal, swollen head, one whorl of 4-5 capitate tentacles, no filiform tentacles, further development unknown.

**DIMENSIONS:** Medusa bell diameter 0.4-0.5 mm, tentacle length up to 1 mm, tentacle capitula diameter 90-110  $\mu$ m. Claparède (1863) reported an egg size of 0.18-0.3 mm, spawned eggs observed in this study were 0.13 mm in diameter. Nematocysts of medusa: stenoteles, (11-27)x(8-19) $\mu$ m, ratio of length to width = 1.5; desmonemes (9-11.5)x(4.5-6) $\mu$ m, r=2.0. Polyp 0.7 mm high, tentacles 0.25 mm long (Drzewina & Bohn, 1913).

**DISTRIBUTION:** French Channel coast, Mediterranean (Naples). Type locality: Tahitou near St. Vaast la Hogue (Normandy, France).

**BIOLOGY:** The medusa was usually found clinging on macroalgae like *Ulva* spec. and *Fucus* spec. in the intertidal zone. In the English Channel, it is most frequent



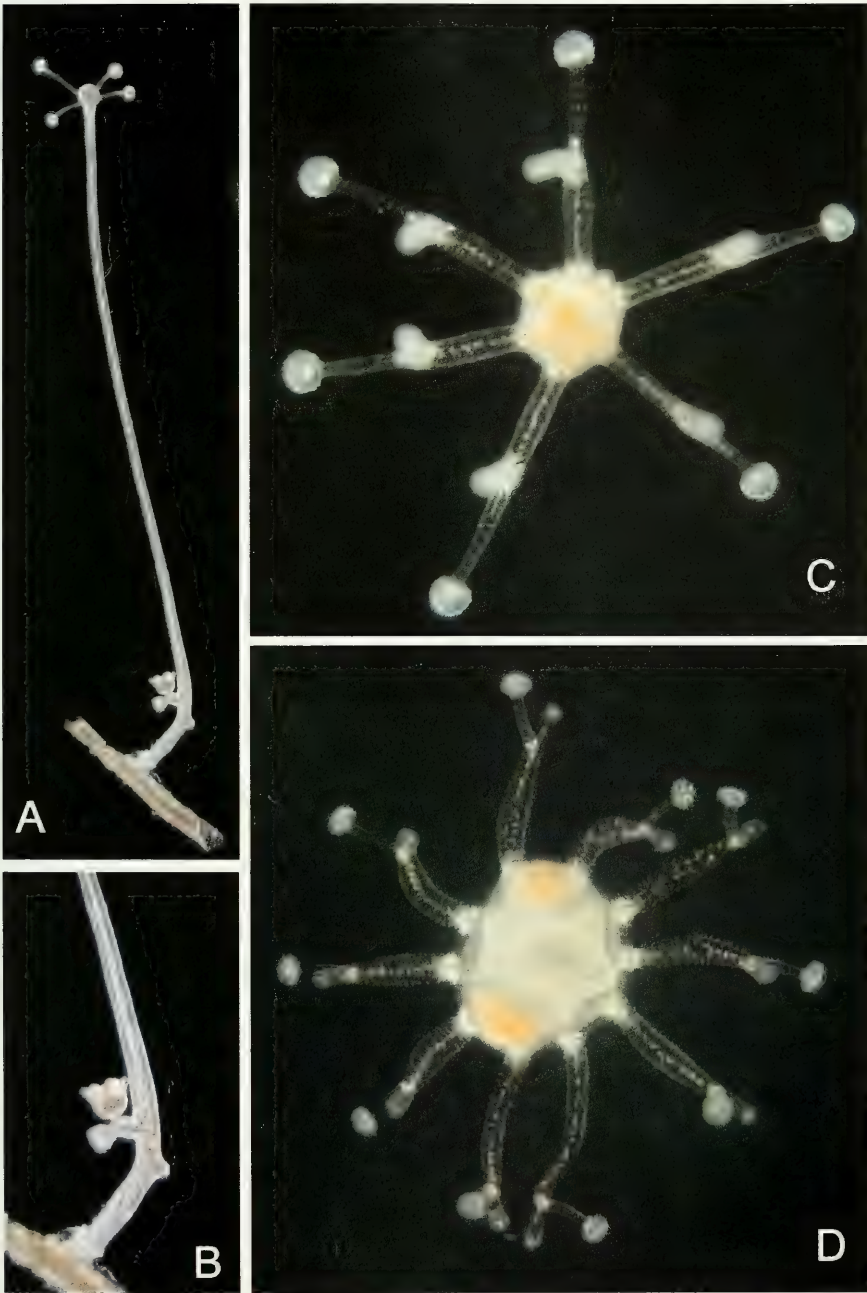


FIG. 19

A) *Eleutheria dichotoma* Quatrefages, 1842, cultivated polyp with medusa bud. B) as in A, enlarged medusa bud on gonostyle. C) *Eleutheria dichotoma*, mature medusa, an egg can be faintly seen. D) *Eleutheria clapedii* Hartlaub, 1889, medusa with two buds in the subumbrella.

in autumn and winter and disappears almost completely in spring (Teissier, 1965). Asexual production occurs all year round but especially during spring time, animals with mature gonads were observed from May to June and September to November.

**ADDITIONAL DATA:** The number of tentacles seems not strictly fixed genetically, as budded medusae may have other tentacle numbers than the mother medusa (Drzwina & Bohn, 1913).

Drzewina & Bohn (1913) examined more than 100 medusae and found that asexual medusae-budding stopped with commencing gonad maturation. One male animal observed for this study, however, had medusae buds and mature gonads. The female animal stopped budding before gonad development.

**REMARKS:** *Eleutheria claparedii* (original spelling) was named by Hartlaub (1889) by referring to a description of Claparède (1863) of an animal the latter had erroneously identified as *E. dichotoma*. Hartlaub (1889) states that he also found this species at Naples. He did not designate type material nor a type locality. As Hartlaub mainly referred to the description of Claparède (1863) based on material from Tahitou near St. Vaast la Hogue (Normandy, France), and as the major other descriptions of this species came from this population (Drzwina & Bohn, 1913; Müller, 1911), this locality is herewith selected as type locality. Hartlaub (1907) introduced the incorrect spelling *E. claparedi*, adopted by most subsequent authors. According to the ICZN [1999, 4<sup>th</sup> ed.; articles 31.1.1 and 31.1.3], the epithet can be formed in both versions, but as the spelling in the original publication was *Eleutheria claparedii*, this spelling must be used.

Before Hartlaub (1889), Haeckel (1879) had already introduced two new names for Claparède's animals: *Eleutheria heteronema* and *Eleutheria diplonema*. Although Haeckel's names are senior synonyms, they have never been used as valid names. Article 23.9.1.1 of the ICZN [1999, 4<sup>th</sup> ed.] is therefore invoked to declare them as invalid and *Eleutheria claparedii* Hartlaub, 1889 the valid name of this species.

*Eleutheria claparedii* was investigated in detail by Drzewina & Bohn (1913) and Lengerich (1923a).

The polyp has not yet been identified in the sea and only the young polyp without medusae buds is known from cultivation experiments. Drzewina & Bohn (1913) found them indistinguishable from young polyps of *E. dichotoma*.

### Genus *Staurocladia* Hartlaub, 1917

**TYPE SPECIES:** *Eleutheria vallentini* Browne, 1902, by designation of Hartlaub (1917).

**SYNONYMS:** *Wandelia* Bedot, 1908; *Cnidonema* Gilchrist, 1919.

**REFERENCES:** Hartlaub (1917); Gilchrist (1919); Browne & Kramp (1939); Kramp (1961); Bouillon (1985); Petersen (1990); Bouillon & Boero (2000).

**DIAGNOSIS:** Hydroid stolonial or sessile, hydranths with an oral whorl of capitate tentacles, with or without aboral filiform tentacles; medusa buds borne singly on hydranth body immediately above filiform tentacles or in similar position when these are absent. Medusa adapted to a crawling and walking mode of life, exceptionally still able to swim; without brood-chamber above manubrium; with or without continuous or interrupted nematocyst ring along margin; gonads around manubrium or developed on

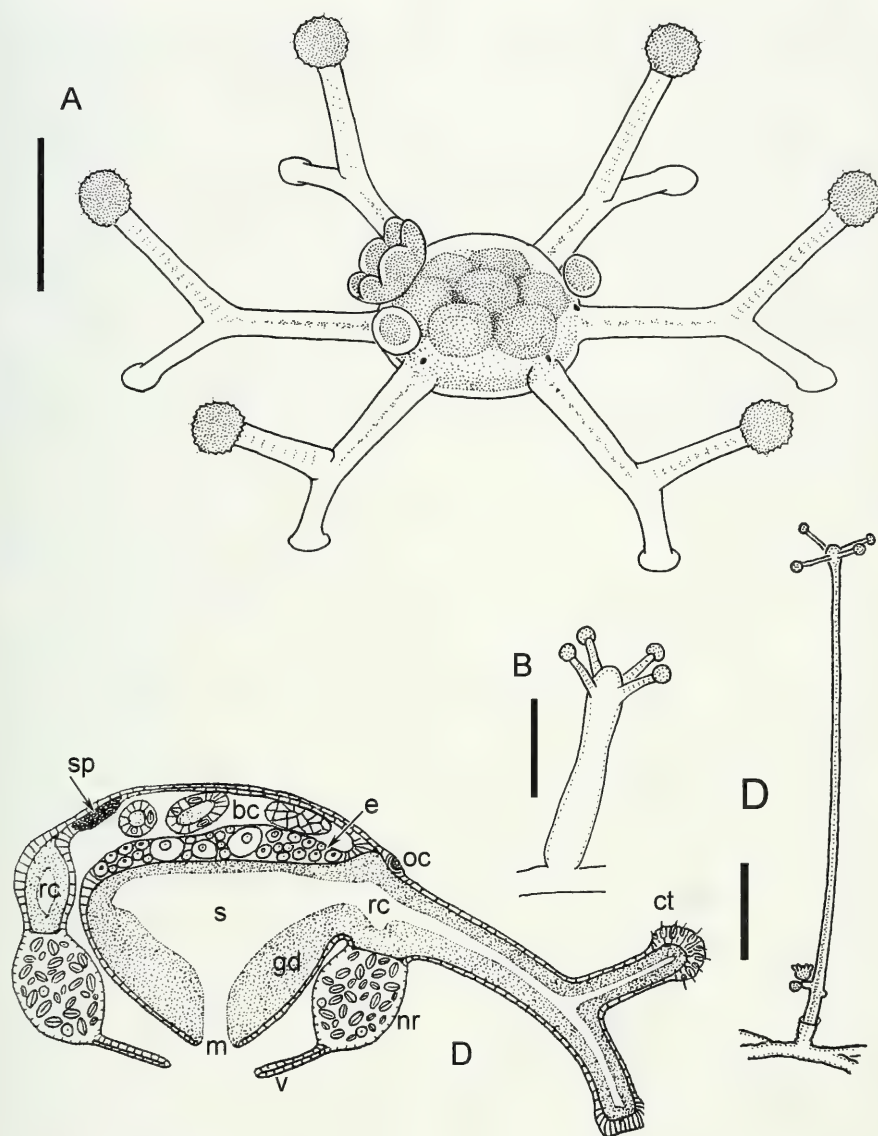


FIG. 20

*Eleutheria dichotoma* Quatrefages, 1842. A) Medusa with developing embryos in brood-chamber, after living material, scale bar 0.5 mm. B) Polyp stage obtained from medusa shown in figure A, scale bar 0.5 mm. C) Polyp with medusae buds, modified after Hauenschild (1956). D) Schematic organization of the medusa in a vertical section, right half perradial, left half interradian; modified after Lengerich (1922). Abbreviations: bc brood-chamber with developing embryos, ct upper branch of tentacle with nematocyst knob (capitulum), e developing eggs, gd gastrodermis, m mouth, nr nettle-ring, oc ocellus, rc radial canal, s stomach, sf lower branch of tentacle with adhesive organ, sp male gonad, v velum.

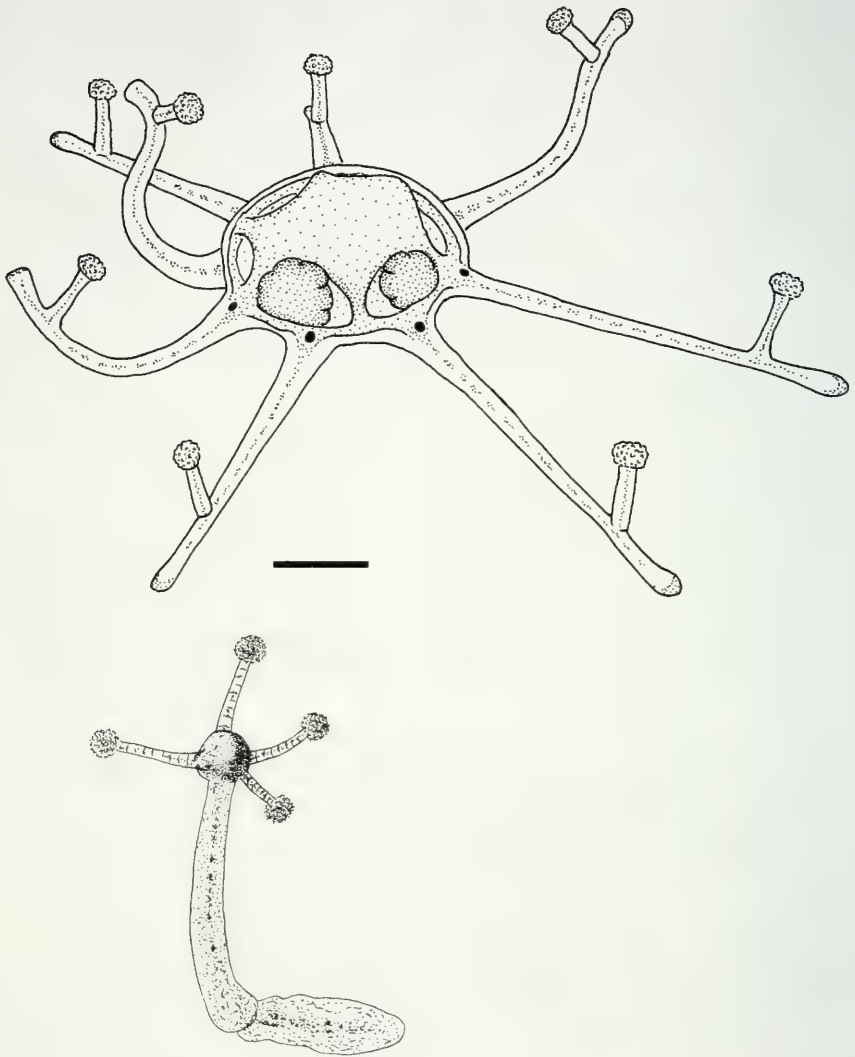


FIG. 21

*Eleutheria clapedii* Hartlaub, 1889. A) after living animal from Roscoff, note the two medusa buds within the subumbrella (stippled darker), scale bar 0.2 mm. B) Young hydranth, after Drzewina & Bohn (1913).

manubrial protrusions; with six to eleven radial canals, some bifurcating shortly distal to manubrium; mouth circular with or without nematocyst knobs; with up to 60 marginal tentacles, dichotomous, upper branch with several nematocyst clusters, lower with adhesive organ; often asexual reproduction by medusa budding or by fission; with abaxial ocelli at tentacle base.



REMARKS: The problems concerning the distinction of *Eleutheria* and *Staurocladia* have been discussed above under "Remarks" at the family level. There is only one species in the European fauna.

***Staurocladia portmanni* Brinckmann, 1964**

Fig. 22

*Staurocladia portmanni* Brinckmann, 1964: 693, figs 1-10; Brinckmann-Voss, 1970: 82, figs 96-98, pl. 6 figs 1-3; Bouillon *et al.*, 2004: 90, fig. 481-J.

MATERIAL EXAMINED: *Staurocladia portmanni*, syntypes BMNH 1963.12.10.2, Ischia, Naples, 2 mature medusae. – *Staurocladia portmanni* syntype BMNH 1963.12.10.1, Italy, Gulf of Sorento, Vico Equense, polyp colony.

DIAGNOSIS: Hydroid with one oral whorl of capitate tentacles and an aboral whorl of six filiform tentacles, short perisarc covered pedicel, medusae budded directly from hydranth body above filiform tentacles. Medusa clinging and creeping on substratum, but also able to swim freely, five to ten branched radial canals, each sending a protuberance into mesogloea, 18-24 tentacles, bifid, nematocyst clusters terminal and on oral and aboral sides of upper branch, plus an additional lateral pair near branching point; five interradian manubrial pouches; gonad surrounds entire manubrium; mouth with five nematocyst clusters.

DESCRIPTION (after Brinckmann, 1964; Brinckmann-Voss, 1970; Bouillon, 1966; and own observations): Hydroid forming small, stolonial colonies. Stolons ensheathed by perisarc which extends up to the short pedicel; hydranth with three to five capitate tentacles in an oral whorl and six filiform tentacles at base of hydranth body, number of filiform tentacles constant; usually one, rarely two medusae buds above filiform tentacles. Preoral cavity present. Nematocysts: stenoteles. Colour: pink-orange. Medusa-bud development very slow, taking up to 50 days.

Newly liberated medusa 0.6-0.7 mm in diameter; seven to nine tentacles, bifid, oral branch with terminal adhesive end, upper branch short and with one terminal nematocyst cluster, sometimes also an additional aboral one, two lateral nematocyst clusters on common trunk near bifurcation always present; five to ten radial canals, number not increasing with further development, protuberances small.

Adult medusa with bell-shaped umbrella, wider than high. Manubrium not extending beyond velum, with five protruding stomach-pouches in middle, mouth with five spherical nematocyst clusters. Gonads surround manubrium and stomach pouches without perradial interruptions, gonads get separated into five sections only where radial canals are adnate to top of the manubrium; gonochoristic, no medusa budding. Five radial canals originating near centre of top of manubrium, then sandwiched between subumbrella and broad base of manubrium for a third of their length, some branching dichotomously so that up to ten radial canals reach the circular canal, at upper third of each radial canal an upright, finger-like protuberance that penetrates into mesogloea; radial canals widen bulb-like before joining circular canal. Tentacles 16-25 in number, hollow, lumen communicates with circular canal; each tentacle bifurcated at about the middle; lower branch with terminal adhesive pad; upper branch with terminal nematocyst cluster (capitulum), plus two to five aboral, and two to four aboral nematocyst clusters; common trunk bears additionally two lateral nematocyst clusters near branching point. Each tentacle contains one basal, abaxial ocellus. Border

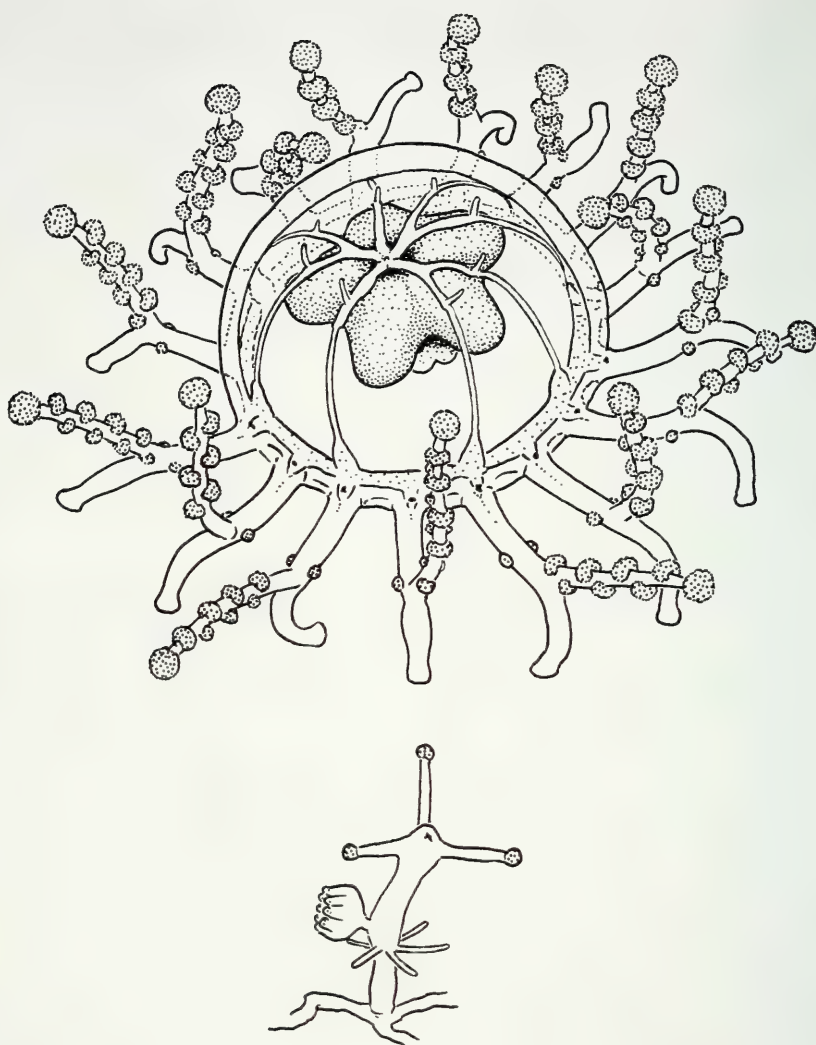


FIG. 22

*Staurocladia portmanni* Brinckmann, 1964, modified after Brinckmann-Voss (1964), above: mature medusa, below: polyp with medusa bud. For size see text.

between exumbrella and velum is thickened with nematocysts. Colours: gastrodermis of stomach, circular canal, and tentacles red-orange; upper part of radial canals and protuberances contain a white pigment, same pigment is also found in the distal part of radial canals where they widen and join circular canal. Nematocysts: stenoteles, desmonemes, and a large, unidentified capsule.

DIMENSIONS: Hydranth body 1.5-2 mm in height, Adult medusa 4-6 mm in diameter, bell-height 2.5-5 mm.

**DISTRIBUTION:** Only known from the region of Naples (Tyrrhenian Sea, Mediterranean). The material used for the original description came from the Gulf of Sorrento (polyp stage) and the island of Ischia (medusa). Under type locality, Brinckmann (1964) gives only the registration number BMNH 1963.12.10.1. According to the label of this specimen in the BMNH, it came from Vico Equense in the Gulf of Sorrento and this locality must therefore be assumed to be the type locality.

**BIOLOGY:** The medusae of *S. portmanni* are found in *Posidonia oceanica* beds in depths of 15-35 m from end of May to begin of July. The hydroid was found on algae like *Udothea* sp. and *Halimeda tuna* in a depth of 30 m. The medusa development is extraordinarily slow, it takes up to 50 days from the first bud to the liberation and another 40-60 to sexual maturity.

The medusa of *S. portmanni* is able to creep as well as to swim freely. More details on its behaviour are given in Brinckmann-Voss (1970).

### Genus *Dendronema* Haeckel, 1879

TYPE SPECIES: *Dendronema stylodendron* Haeckel, 1879 by monotypy.

REFERENCES: Haeckel (1879); Kramp (1961); Bouillon & Boero (2000).

**DIAGNOSIS:** Cladonematidae with branched oral tentacles; umbrella bell-shaped, with an apical cavity above manubrium.

**REMARKS:** A problematic genus containing a single, doubtful species, see discussion below.

### *Dendronema stylodendron* Haeckel, 1879

Fig. 23

*Dendronema stylodendron* Haeckel, 1879: 110, pl. 7 fig. 8; Lengerich, 1922: 210; Kramp, 1955: 307; Kramp, 1959: 96; Kramp, 1961: 58.

**MATERIAL:** None examined, likely no type material exists.

**DIAGNOSIS:** As for genus.

**DESCRIPTION** (after Haeckel, 1879): Umbrella bell shaped, height 9 mm, diameter 6 mm; with pointed, conical apical process, nearly twice as high as broad. Manubrium spindle-shaped, continued into mesogloea as apical cavity, in proximal half with four egg-shaped gonads, mouth with four dichotomously branched oral tentacles (50-60 ends) reaching down to velum level. Four radial canals that divide close to manubrium into two branches. Eight tentacles, each with an ocellus that has a lens, each tentacle divided into two principal branches, of which the adaxial one branches two times and bears four adhesive ends, the abaxial branch divides dichotomously several times and bears many nematocyst knobs. Colours: manubrium and apical cavity reddish-yellow; tentacles, radial- and circular canals red; ocelli black.

**DISTRIBUTION:** Known from original description only, type locality: Lanzarote, Canary Islands.

**REMARKS:** Besides its first description, *Dendronema stylodendron* has never been reported again and some authors doubted its existence, e. g. Lengerich (1923a) lists it as a synonym of *Cladonema radiatum*. Kramp (1955, 1961) thought that this is

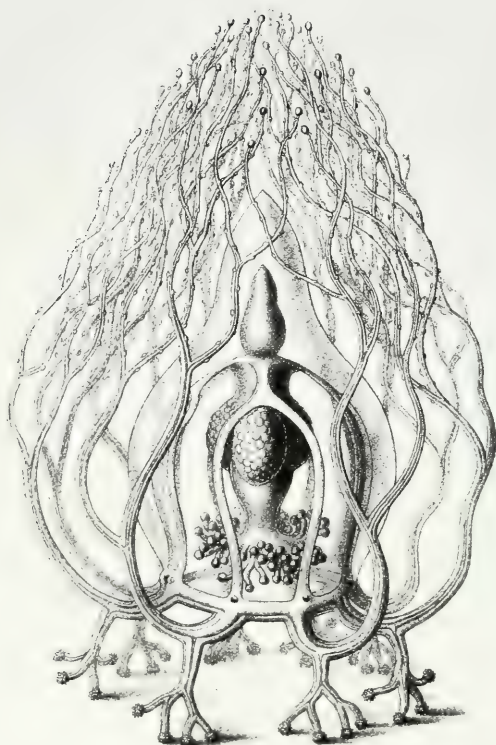


FIG. 23

*Dendronema stylodendron*, after Haeckel 1879.

unlikely, but nevertheless classified it as doubtful (Kramp, 1959). Haeckel based his description of on a living specimen he collected at Lanzarote. The animal is remarkably large for this family and his drawings are quite detailed. So, it seems quite unlikely that Haeckel confounded it with the much smaller *Cladonema radiatum*. However, the species remains somewhat doubtful until it can be found again.

#### ACKNOWLEDGEMENTS

This study was made possible through a SYNTHESIS grant of the European Union that enabled me to examine hydrozoans of the Natural History Museum in London. I also wish to express my sincere thanks to the museums of Copenhagen, Bergen, Bruxelles, and Hamburg which provided valuable loans of material. Many thanks are also due to Dr B. Schierwater who provided a culture of *E. dichotoma*, Dr M. Stierwald who provided photos of *Cladonema radiatum*, and Dr W. Vervoort who gave me valuable taxonomic advice on the validity of *C. cocksii*. Mrs J. Pralong kindly made the serial histological sections. I would also like to thank Dr F. Boero, Dr D. Calder, and Dr A. Marques who commented on initial versions of the manuscript. However, this is not meant to delegate my responsibility for the content and all shortcomings and errors are mine alone.



## REFERENCES

- ACHERMANN, J. & TARDENT, P. 1973. Untersuchungen zum Problem des Nematocyten-Nachschubs bei *Cladonema radiatum* (Hydrozoa). *Revue suisse de Zoologie* 80: 704-712.
- AGASSIZ, L. 1862. Contributions to the Natural History of the United States of America. Vol. IV. *Little Brown, Boston*, pp. 1-380, pls 1-19.
- ALLMAN, G. J. 1871-1872. A monograph of the gymnoblastic or tubularian hydroids. Conclusion of Part I, and Part II, containing descriptions of the genera and species of Gymnoblastea. *Ray Society, London*, pp. 155-450, 23 plates.
- ALLMAN, G. J. 1874. Notes on the structure and development of *Myriothele phrygia*. *Annals and Magazine of Natural History* (4)14: 317-321.
- ALLMAN, G. J. 1876. On the structure and development of *Myriothele*. *Philosophical Transactions of the Royal Society of London* (B)165: 549-575, pls 55-58.
- ALLMAN, G. J. 1888. Report on the Hydroida dredged by H. M. S. Challenger during the years 1873-76. Part II.- The Tubularinae, Corymorphinae, Campanularinae, Sertularinae, and Thalamophora. *The Voyage of H. M. S. Challenger, Zoology* 23: 1-90.
- ANTSULEVICH, A. E. 1988. The first finding of hydroids of the genus *Monocoryne* (Hydrozoa, Myriotheleidae) in the waters of the USSR. *Zoologicheskii Zhurnal* 67: 931-933.
- ANTSULEVICH, A. E. & POLTEVA, D. G. 1986. Hydroids of the genus *Rhizogeton* (Athecata, Clavidae) in fauna of the USSR. *Zoologicheskii Zhurnal* 65: 965-972.
- AURIVILLIUS, C. W. S. 1898. Vergleichende Thiergeographische Untersuchungen über die Plankton-Fauna des Skageraks in den Jahren 1893-97. *Kongliga Svenska Vetenskaps-Akademiens Handlingar* 30: 1-427.
- AYRES, W. O. 1854. A description of a new species of polyp from Long Island, allied to *Tubularia*, under the name *Globiceps tiarella* Ayres. *Proceedings of the Boston Society of Natural History* 4: 193-196.
- BAKER, E. G. S. 1936. Photoperiodicity in the spawning reaction of *Pennaria tiarella* McCr. *Proceedings of the Indian Academy of Science* 45: 251-252.
- BAKER, R. J. 1913. *Protohydra Leuckartii* in tidal pools of River Tavy. *Transactions of the Plymouth District Field Council* 1: 23.
- BARNES, R. S. K. 1994. The brackish-water fauna of northwestern Europe: an identification guide to brackish-water habitats, ecology and macrofauna for field workers, naturalists and students. *Cambridge University Press, Cambridge*, pp. XVI + 287.
- BEDOT, M. 1901. Matériaux pour servir à l'histoire des hydroïdes. 1re période. *Revue suisse de Zoologie* 9: 379-515.
- BEDOT, M. 1908. Sur un animal pélagique de la région antarctique. *Expédition antarctique Française (1903-1905), Spongiaires et Coelentérés* 3: 1-7, plate.
- BEDOT, M. 1911. Notes sur les hydroïdes de Roscoff. *Archives de Zoologie Expérimentale et Générale* 6: 201-228.
- BEDOT, M. 1912. Matériaux pour servir à l'histoire des hydroïdes. 4e période (1872-1880). *Revue suisse de Zoologie* 20: 213-469.
- BEDOT, M. 1916. Matériaux pour servir à l'histoire des hydroïdes. 5e période (1881-1890). *Revue suisse de Zoologie* 24: 1-349.
- BEDOT, M. 1918. Matériaux pour servir à l'histoire des hydroïdes. 6e période (1891-1900). *Revue suisse de Zoologie* 26, supplement: 1-376.
- BEIGEL, U. 1976. Gonophorenentwicklung der Hydroide *Myriothele*. *Cahiers de Biologie Marine* 17: 119-129, pls 1-4.
- BEIGEL-HEUWINKEL, U. 1984. Zur Eientwicklung bei *Myriothele cocksi* (Hydrozoa, Athecata). *Verhandlungen der Deutschen Zoologischen Gesellschaft* 77: 273.
- BEIGEL-HEUWINKEL, U. 1982a. Helical fibrils in the mesoglea of a hydropolyp. *Tissue & Cell* 14: 225-230.

- BEIGEL-HEUWINKEL, U. 1982b. Experiments and observations on regeneration in *Myriothele cocksi*. *Acta Zoologica* 63: 199-210.
- BEIGEL-HEUWINKEL, U. 1988. Brutpflege bei den marinen Hydroidpolypen *Myriothele cocksi* (Vigurs), mit Hilfe spezieller Tentakel. *Acta biologica Benrodis* 1: 56-67.
- BENOÎT, P. 1923a. L'ovogénèse et la segmentation de *Myriothele Cocksii* (Vigurs). *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences, Paris* 176: 1836-1838.
- BENOÎT, P. 1923b. Le gonophore hermaphrodite de *Myriothele cocksi* (Vigurs). *Comptes rendus hebdomadaires des séances et mémoires de la Société de biologie et de ses filiales et associées* 89: 507-510.
- BENOÎT, P. 1925. L'ovogénèse et les premiers stades du développement chez la Myriothele et chez la Tubularie. *Archives de Zoologie Expérimentale et Générale* 64: 85-326.
- BERRILL, N. J. 1952. Growth and form in gymnoblastic hydroids. II. Sexual and seasonal reproduction in *Rathkea*. III. Hydranth and gonophore development in *Pennaria* and *Acaulis*. IV. Relative growth in *Eudendrium*. *Journal of Morphology* 90: 1-32.
- BILLARD, A. 1905. Note complémentaire sur les hydroides de la Baie de la Hougue. *Bulletin du Muséum national d'histoire naturelle, Paris* 11: 500-502.
- BILLARD, A. 1921. Note sur la biologie et la régénération de la Myriothele. *Bulletin de la Société Zoologique de la France* 46: 12-17.
- BOADEN, P. J. S. 1976. Soft meiofauna of sand from the delta region of the Rhine, Meuse and Scheldt. *Netherlands Journal of Sea Research* 10: 461-471.
- BODO, F. 1970. Étude du développement embryonnaire de l'anthoméduse *Cladonema radiatum* Dujardin (Athécate, Capitée, Cladonematidée). *Annales d'embryologie et de morphogénèse* 3: 309-313.
- BOERO, F. & FRESI, E. 1986. Zonation and evolution of a rocky bottom hydroid community. *Marine Ecology* 7: 123-150.
- BOERO, F. 1981. Systematics and ecology of the hydroid population of two *Posidonia oceanica* Meadows. *Marine Ecology* 2: 181-197.
- BONNEVIE, K. 1898a. Zur Systematik der Hydroiden. *Zeitschrift für Wissenschaftliche Zoologie* 63: 465-495, plates 25-27.
- BONNEVIE, C. 1898b. Neue norwegische Hydroiden. *Bergens Museum Årbok* 5: 1-16, plates 1-2.
- BONNEVIE, K. 1899. Hydroida. *Norske Nordhavs-Expedition 1876-1878, Zoologi* 26: 1-104, pls 1-8, map.
- BOSC, L. A. G. 1797. Description des objets nouveaux d'histoire naturelle trouvés dans une traversée de Bordeaux à Charles-Town. *Bulletin des Sciences, par la Société philomatique de Paris* 1(2): 9-10.
- BOUILLON, J. 1965. In: Tessier (1965).
- BOUILLON, J. 1966. Les cellules glandulaires des Hydroides et Hydroméduses. Leur structure et la nature de leurs sécrétions. *Cahiers de Biologie Marine* 7: 157-205.
- BOUILLON, J. 1968. Sur la structure des tentacules adhésifs des Cladonematidae et Eleutheriidae (Anthomedusae). *Pubblicazioni della Stazione Zoologica di Napoli* 36: 471-504.
- BOUILLON, J. 1966. Les cellules glandulaires des Hydroides et Hydroméduses. Leur structure et la nature de leurs sécrétions. *Cahiers de Biologie Marine* 7: 157-205.
- BOUILLON, J. 1971. Sur quelques hydroides de Roscoff. *Cahiers de Biologie Marine* 12: 323-364.
- BOUILLON, J. 1974. Description de *Teissiera milleporoides*, nouveau genre et nouvelle espèce de Zancleidae des Seychelles (Hydrozoaires; Athecates-Anthomédues), avec une révision des Hydroides "Pteronematoidea". *Cahiers de Biologie Marine* 15: 113-154.
- BOUILLON, J. 1985. Essai de classification des hydropolypes-hydroméduses (Hydrozoa-Cnidaria). *Indo-Malayan Zoology* 2: 29-243.
- BOUILLON, J. 1994. Les Hydrozoaires (pp. 29-416). In: P. GRASSÉ & J. DOUMENG (eds). *Traité de Zoologie. Masson, Paris*.
- BOUILLON, J., BOERO, F. & SEGHERS, G. 1987. Redescription of *Cladocoryne haddoni* Kirkpatrick and a proposed phylogeny of the superfamily Zancleioidea (Anthomedusae, Hydrozoa, Cnidaria). *Indo-Malayan Zoology* 4: 279-292.
- BOUILLON, J., BOERO, F. & SEGHERS, G. 1988. Notes additionnelles sur les Hydroméduses de la mer de Bismarck (Hydrozoa-Cnidaria) 2. *Indo-Malayan Zoology* 5: 87-99.

- BOUILLON, J., MASSIN, C. & KRESEVIC, R. 1995. Hydroidomedusae of the Belgian Royal Society of Natural Sciences. *Institut Royal Des Sciences Naturelles de Belgique Documents de Travail* 78: 1-106.
- BOUILLON, J. & HOUVENAGHEL, G. 1970. Histophysiologie et la digestion chez *Cladonema radiatum*, Dujardin, 1843. *Pubblicazioni della Stazione Zoologica di Napoli* 38: 71-108.
- BOUILLON, J. & BOERO, F. 2000. Synopsis of the families and genera of the Hydromedusae of the world, with a list of the worldwide species. *Thalassia Salentina* 24: 47-296.
- BOUILLON, J., MEDEL, M. D., PAGÈS, F., GILI, J. M., BOERO, B. & GRAVILI, C. 2004. Fauna of the Mediterranean Hydrozoa. *Scientia Marina* 68(Suppl. 2): 1-448.
- BOZHENOVA, O. V., STEPANJANTS, S. D. & SHEREMETEVSKY, A. M. 1989. The first finding of the meiobenthic Cnidaria *Boreohydra simplex* (Hydrozoa, Athecata) in the White Sea. *Zoologicheskii Zhurnal* 68: 11-16.
- BRIEN, P. 1941. Remarques au sujet des conceptions relatives à l'existence et à la pérennité, chez les Hydroïdes, d'une réserve embryonnaire et d'une lignée germinale, à propos du bourgeonnement et des potentialités de l'ectoderme de "*Cladonema radiatum*" (Duj.). *Annales de la Société royale zoologique de Belgique* 72: 37-62.
- BRIEN, P. 1942. Étude sur deux hydroides gymnoblastiques *Cladonema radiatum* (Duj.) et *Clava squamata* (O.F. Müller) (Origine des cellules blastogénétiques, sexuelles, des cnidoblastes et des cellules glandulaires. Le polype, la méduse, le gonophore). *Mémoires de l'Académie royale de Belgique, Classe des sciences* 20: 1-116.
- BRINCKMANN, A. 1964. Observations on the biology and development of *Staurocladia portmanni* sp. n. (Anthomedusae, Eleutheridae). *Canadian Journal of Zoology* 42: 693-706, pls 1-2.
- BRINCKMANN, A. 1966. The morphology and development of *Acaulis ilonae* sp. nov. (order Anthomedusae-Athecatae, Fam. Acaulidae). *Canadian Journal of Zoology* 44: 291-301.
- BRINCKMANN-VOSS, A. 1970. Anthomedusae/Athecata (Hydrozoa, Cnidaria) of the Mediterranean. Part I. Capitata. *Fauna e Flora Golfo di Napoli* 39: 1-96, pls 1-11.
- BRINCKMANN, A. & PETERSEN, K. W. 1960. On some distinguishing characters of *Dipurena reesi* Vannucci 1956 and *Cladonema radiatum* Dujardin 1843. *Pubblicazioni della Stazione Zoologica di Napoli* 31: 386-392.
- BROCH, H. 1903. Die vom norwegischen Fischereidampfer "Michael Sars" in den Jahren 1900-1902 in dem Nordmeer gesammelten Hydroiden. *Bergens Museums Aarbog* (1903) 9: 1-14, pls 1-4, table.
- BROCH, H. 1910. Die Hydroiden der Arktischen Meere. *Fauna Arctica* 5: 127-248, plates 2-4.
- BROCH, H. 1916. Hydroida. (Part I). *Danish Ingolf Expedition* 5: 1-66.
- BROWNE, E. T. 1900. Report on the Medusae. The fauna and flora of Valencia Harbour on the west coast of Ireland. *Proceedings of the Royal Irish Academy* (3)5: 694-736, pls 20-21.
- BROWNE, E. T. 1902. A preliminary report on Hydromedusae from the Falkland islands. *Annals and Magazine of natural History* (7) 9: 272-284.
- BROWNE, E. T. 1903. Report on some medusae from Norway and Spitzbergen. *Bergens Museum Aarbog* 4: 1-36.
- BROWNE, E. T., & KRAMP, P. L. 1939. Hydromedusae from the Falkland Islands. *Discovery Reports* 18: 265-322.
- BRUMWELL, G. B. & MARTIN, V. J. 1996. Ultrastructural localization of RFamide-like peptides in neuronal dense-cored vesicles of a cnidarian planula larva. *Invertebrate Biology* 115: 13-19.
- CALDER, D. R. 1974. The mud-dwelling hydrozoan *Boreohydra simplex* in the western North Atlantic. *Journal of the Fisheries Research Board of Canada* 31: 1666-1667, pl. 1.
- CALDER, D. R. 1988. Shallow-water hydroids of Bermuda. The Athecatae. *Royal Ontario Museum Life Sciences Contributions* 148: 1-107.
- CALDER, D. R., MALLINSON, J. J., COLLINS, K. & HICKMAN, C. P. 2003. Additions to the hydroids (Cnidaria) of the Galapagos, with a list of species reported from the islands. *Journal of Natural History* 37: 1173-1218.



- CASTRIC-FEY, A. 1970. Sur quelques hydraires de l'Archipel de Glénan (Sud-Finistère). *Vie et Milieu* 21: 1-23.
- CERFONTAINE, P. 1902. Recherches expérimentales sur la régénération et l'hétéromorphose chez *Astroïdes calycularis* et *Pennaria cavolinii*. *Archives de Biologie, Paris* 19: 245-315.
- CHRISTIANSEN, B. O. 1972. The hydroid fauna of the Oslo Fjord in Norway. *Norwegian Journal of Zoology* 20: 279-310.
- CLAPARÈDE, R. E. 1863. Beobachtungen über Anatomie und Entwicklungsgeschichte wirbelloser Thiere an der Küste von Normandie angestellt. *Wilhelm Engelmann, Leipzig*, pp. 120, 18 plates.
- CLARK, S. D. & COOK, C. B. 1986. Inhibition of nematocyst discharge during feeding in the colonial hydroid *Halocordyle disticha* (= *Pennaria tiarella*): the role of previous prey-killing. *Biological Bulletin* 171: 405-416.
- CLAUSEN, C. 1971. Interstitial Cnidaria: present status of their systematics and ecology. *Smithsonian Contributions to Zoology* 76: 1-8.
- CLAUSEN, C. & VON SALVINI-PLAWEN, L. 1986. Cnidaria (pp. 33-42). In: BOTOSANEANU, L. (ed). *Stygofauna Mundi*, A faunistic, distributional, and ecological synthesis of the worldfauna inhabiting subterranean waters (including the marine interstitial). *Brill/Dr. W. Backhuys, Leiden*, pp. i-vi, 1-740.
- COCKS, W. P. 1850. Contributions to the fauna of Falmouth. *Annual Report of the Royal Cornwall Polytechnic Society* 17: 38-103. [publication year 1850 according to Cornelius (1977)]
- COCKS, W. P. 1853. *Spadix purpurea*, Gosse. *Annals and Magazine of Natural History* (2) 12: 365.
- COCKS, W. P. 1854. Contributions to the Falmouth Fauna. *Annual Report of the Royal Cornwall Polytechnic Society* 20: 1-68. [publication year 1854 according to Cornelius (1977)]
- COLLINS, A. G., WINKELMANN, S. & SCHIERWATER, B. 2005. An assessment of partial mitochondrial 16S rDNA sequences as indicators of Corynidae (Hydrozoa, Anthoathecata) phylogeny. *Zoologica Scripta* 34, 91-99.
- COLLINS, A. G., SCHUCHERT, P., MARQUES, A. C., JANKOWSKI, T., MEDINA, M. & SCHIERWATER, B. 2005. Cnidarian Phylogeny and Character Evolution Clarified by New Large and Small Subunit rDNA Data and an Assessment of the Utility of Phylogenetic Mixture Models. *Systematic Biology*, in press.
- COOKE, W. J. 1977. Order Hydroida. *Bernice P. Bishop Museum Special Publication* 64: 71-104.
- CORNELIUS, P. F. S. 1977. On the nomenclature of the hydroid, *Candelabrum phrygium* (Fabricius, 1780) (= *Myriothele phrygia*, *Arum cocksii*). *Journal of the Marine Biological Association of the U. K.* 57: 521-524.
- CORNELIUS, P. F. S. 1992. The Azores hydroid fauna and its origin, with discussion of rafting and medusa suppression. *Arquipelago Ciencias da Natureza* 10: 75-99.
- COSTELLO, M. J., EMBLOW, C. & WHITE R. (eds) 2001. European Register of Marine Species. A check-list of marine species in Europe and a bibliography of guides to their identification. *Patrimoines naturels* 50, 1-463. Available online at: <http://www.MarBEF.org/data/erms.php>.
- COWDEN, R. R. 1964. A cytochemical study of gonophore and oocyte development in *Pennaria tiarella*. *Acta embryologiae et morphologiae experimentalis* 7: 167-179.
- COWDEN, R. R. 1965a. A cytological and cytochemical study of hydranths of the hydroid coelenterate, *Pennaria tiarella*. *Zeitschrift für Zellforschung und mikroskopische Anatomie* 65: 869-883.
- COWDEN, R. R. 1965b. Cytochemical studies of embryonic development to metamorphosis in the gymnoblastic hydroid, *Pennaria tiarella*. *Acta embryologiae et morphologiae experimentalis* 8: 221-231.
- DA CUNHA, A. X. 1944. Hidropólipos das costas de Portugal. *Memorias e Estudos de Museu Zoológico da Universidade de Coimbra* 161: 1-101.



- DA SILVEIRA, F. L. & MIGOTTO, A., E. 1991. The variation of *Halocordyle disticha* (Cnidaria, Athecata) from the Brazilian coast: an environmental indicator species? *Hydrobiologia* 216/217: 437-422.
- DALY YAHIA, M. N., GOY, J. & DALY YAHIA-KÉFI, O. 2003. Distribution et écologie des Méduses (Cnidaria) du golfe de Tunis (Méditerranée sud occidentale). Distribution and ecology of Medusae and Scyphomedusae (Cnidaria) in Tunis Gulf (SW Mediterranean). *Oceanologica Acta* 26: 645-655.
- DAWYDOFF, C. N. 1930. *Protohydra caulleryi*, nov. sp., des eaux indochinoises. *Archives de Zoologie Expérimentale et Générale, notes et revue* 70: 55-57.
- BLAINVILLE, H. M. DE 1830. Zoophytes (pp. 326). In: CUVIER, F. (ed.). Dictionnaire des sciences naturelles. Volume 60. *Levrault and Le Normant, Strasbourg & Paris*. 72 volumes.
- DE FILIPPI, F. 1866. Sopra due Idrozoi del Mediterraneo. *Memorie della Reale Accademia delle Scienze di Torino, Scienze fisiche e matematiche Serie 2* vol. 23: 375-385.
- DENDY, A. C. 1902. On a free-swimming hydroid, *Pelagohydra mirabilis* n. gen. et sp. *The quarterly journal of microscopic science* 46: 1-24, plates 1-2.
- DRZEWINA, A. & BOHN, G. 1913. Observations biologiques sur *Eleutheria dichotoma* et *E. claredei*. *Archives de Zoologie Expérimentale et Générale* 53: 15-59.
- DU PLESSIS, G. 1880. Observations sur la *Cladocoryne* floconneuse (*Cladocoryne floccosa*, Rotch.). *Bulletin de la Société vaudoise des Sciences naturelles* (2)17: 119-144, pl. 10.
- DU PLESSIS, G. 1909. Note sur l'élevage des Eleutheries de la Méditerranée au moyen de l'isolement. *Revue suisse de Zoologie* 17: 371-377.
- DUJARDIN, F. 1843. Observations sur un nouveau genre de médusaires provenant de la métamorphose des Syncorynes. *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences, Paris* 16: 1132-1136.
- DUJARDIN, F. 1845. Mémoire sur le développement des Méduses et des Polypes Hydriques. *Annales des Sciences Naturelles, Paris* (3), *Zoologie* 4: 257-280.
- EHRENBERG, C. G. 1834. Beiträge zur physiologischen Kenntnis der Corallenthiere im allgemeinen, und besonders des rothen Meeres, nebst einem Versuche zur physiologischen Systematik derselben. *Abhandlungen der Königlichen Akademie der Wissenschaften, Berlin* 1: 225-380.
- ENDER, A. 1997 Untersuchungen zur Evolutionsgenetik des athekaten Hydrozoons *Eleutheria dichotoma* (Quatrefages 1842). *PhD Thesis Fachbereich Biologie, Johan Wolfgang Goethe Universität Frankfurt*, 103 pp.
- ESCHSCHOLTZ, F. 1829. System der Acalephen. Eine ausführliche Beschreibung aller medusenartigen Strahlthiere. *Ferdinand Dümmler, Berlin*, 190 pp.
- EVERTSEN, J., BAKKEN, T. & GREEN, S. 2004. Rediscovery of *Tenellia adspersa* (Nudibranchia) from the Finnish archipelago. *Sarsia* 89: 362-365.
- FABRICIUS, O. 1780. Fauna Groenlandica. *G. Rothe, Hafniae and Lipsiae*, pp. 1-452, plate 1.
- FALUGI, C., MORRI, C., BOUILLON, J., & BOERO, F. 1994. Localization of some neurotransmitters during development in hydroidomedusae. *Tissue & Cell* 26: 523-538.
- FEWKES, J. W. 1890. A zoological reconnaissance in Grand Manan. *American Naturalist* 24: 432-438.
- FORBES, E. 1848. A monograph of the British naked-eyed medusae: with figures of all the species. *Ray Society, London*, pp. 104, 13 plates.
- FRASER, C. M. 1924. *Acaulis primarius* Stimpson. *Transactions of the Royal Society of Canada, Sec. V* 173: 165-173.
- FRASER, C. M. 1938. Hydroids of the 1932, 1933, 1935 and 1938 Allan Hancock Pacific Expeditions. *Allan Hancock Pacific Expeditions* 4: 129-153.
- FRASER, C. M. 1941. New species of hydroids, mostly from the Atlantic Ocean, in the United States National Museum. *Proceedings of the United States National Museum* 91: 77-89.
- FRASER, C. M. 1944. Hydroids of the Atlantic coast of North America. *The University of Toronto Press, Toronto*, pp. 1-451, pls 1-94.

- FRASER, C. M. 1948. Hydroids of the Allan Hancock Pacific Expeditions since March, 1938. *Allan Hancock Pacific Expeditions* 4: 179-343.
- FRIEDRICH, H. 1961. Die Hydromeduse *Eleutheria dichotoma* Quatrefages im Litoral der Atlantischen Insel Madeira. *Bocagiana* 8: 1.
- GARCIA CORRALES, P. & AGUIRRE, A. 1985. La especie *Halocordyle disticha* (Goldfuss, 1820), y sus sinonimias. *Boletín del Instituto Español de Oceanografía* 2: 85-96.
- GAST, R. & GODLEWSKI, E. 1903. Die Regulationserscheinungen bei *Pennaria cavolinii*. *Archiv für Entwicklungsmechanik der Organismen* 16: 76-116.
- GEGENBAUR, C. 1856. Versuch eines Systems der Medusen, mit Beschreibung neuer oder wenig gekannter Formen; zugleich ein Beitrag zur Kenntnis der Fauna des Mittelmeeres. *Zeitschrift für wissenschaftliche Zoologie, Leipzig* 8: 202-273, pls 7-9.
- GENZANO, G. N. & KUBOTA, S. 2003. Synchronous mass release of mature medusae from the hydroid *Halocordyle disticha* (Hydrozoa, Halocordylidae) and experimental induction of different timing by light changes. *Publications of the Seto Marine Biological Laboratory* 39: 221-228.
- GIBBONS, M. J. & RYLAND, J. S. 1989. Intertidal and shallow water hydroids from Fiji. 1. Athecata to Sertulariidae. *Memoirs of the Queensland Museum* 27: 377-432.
- GILCHRIST, J. D. F. 1919. On a species of the crawling medusa, *Eleutheria*, from the Cape of Good Hope (*Cnidonema capensis* g. et sp. n.) and the southern Eleutheridae. *Quarterly Journal of microscopical Science* 63: 509-529.
- GOLDFUSS, G. A. 1820. Handbuch der Zoologie. Erste Abteilung. Schrag, Nürnberg, pp. 1-696.
- GOSSE, P. H. 1853a. Notes on some new or little-known marine animals. *Annals and Magazine of Natural History* (2)12: 124-128.
- GOSSE, P. H. 1853b. Notes on some new or little-known marine animals. *Annals and Magazine of Natural History* (2)12: 153-159.
- GOSSE, P. H. 1853c. Notes on some new or little-known marine animals. *Annals and Magazine of Natural History* (2)12: 384-386.
- GOSSE, P. H. 1853d. A naturalist's rambles on the Devonshire coast. *John van Voorst, London*, pp. xvi+451, 28 plates.
- GRAEFFE, E. 1883a. Ueber *Polycoryne Helleri* eine neue Corynidengattung. *Bolletino della Società Adriatica di Scienze Naturali in Trieste* 8: 202-205.
- GRAEFFE, E. 1883b. Nachtrag zu dem Aufsatz über *Polycoryne Helleri*. *Bolletino della Società Adriatica di Scienze Naturali in Trieste* 8: 320.
- GREEFF, R. 1869. *Protohydra Leuckarti*. Eine marine Stammform der Coelenteraten. *Zeitschrift für wissenschaftliche Zoologie* 20: 37-54, pl. 4-5.
- GÜNTHER, R. T. 1903. On the structure and affinities of *Mnestra parasites* Krohn, with a revision of the classification of the Cladonemidae. *Mitteilungen aus der Zoologischen Station zu Neapel* 16: 35-62.
- HADRY, H., SCHIERWATER, B. & MROWKA, W. 1990. The feeding behaviour of a semi-sessile hydromedusa and how it is affected by the mode of reproduction. *Animal Behaviour* 40: 935-944.
- HAECKEL, E. 1879. Das System der Medusen. Erster Teil einer Monographie der Medusen. *Denkschriften der Medicinisch-Naturwissenschaftlichen Gesellschaft zu Jena* 1: XX+360 pp., 20 plates.
- HAMOND, R. 1964. Further notes on the Hydrozoa of the Norfolk coast. *Annals and Magazine of Natural History* 13: 659-670.
- HARDY, W. B. 1891. On some points in the histology and development of *Myriothele phrygia*. *Quarterly journal of microscopical Science* n. ser. 32: 506-537.
- HARGITT, C. W. 1899. Early development of *Pennaria tiarella*. *Science, N.Y.* n. ser. 9: 368-369.
- HARGITT, C. W. 1900. A contribution to the natural history and development of *Pennaria tiarella* McCr. *American Naturalist* 34: 387-414, pls 1-4.

- HARGITT, C. W. 1904. The early development of *Pennaria tiarella* McCr. *Archiv für Entwicklungsmechanik der Organismen* 18: 453-488.
- HARGITT, G. T. 1909. Maturation, fertilization, and segmentation of *Pennaria tiarella* (Ayres) and of *Tubularia crocea* (Ag.). *Bulletin of the Museum of Comparative Zoölogy / Harvard University* 53: 159-212.
- HARGITT, C. W. 1927. Some hydroids of South China. *Bulletin of the Museum of Comparative Zoölogy of Harvard College* 67: 491-520.
- HARTLAUB, C. 1886. Ueber den Bau der *Eleutheria* Quatref. *Zoologischer Anzeiger* 9: 706-711.
- HARTLAUB, C. 1887. Zur Kenntnis der Cladonemiden. Zweite vorläufige Mittheilung. *Zoologischer Anzeiger* 10: 651-658.
- HARTLAUB, C. 1889. Ueber die Claparède'sche "*Eleutheria*". *Zoologischer Anzeiger* 12: 665-671.
- HARTLAUB, C. 1897. Die Hydromedusen Helgolands. *Wissenschaftliche Meeresuntersuchungen* 2: 449-536, pls 14-23.
- HARTLAUB, C. 1899. Zur Kenntnis der Gattungen *Margelopsis* und *Nemopsis*. *Nachrichten von der Gesellschaft der Wissenschaften zu Göttingen. Mathematisch-physikalische Klasse* 1899: 219-224.
- HARTLAUB, C. 1903. Dendy, A., On a free-swimming hydroid, *Pelagohydra mirabilis* n. g., n. sp. *Zoologisches Zentralblatt* 10: 27-34.
- HARTLAUB, C. 1907. XII Craspedote Medusen. Teil 1, Lief. 1. Codoniden und Cladonemiden. *Nordisches Plankton* 6: 1-135.
- HARTLAUB, C. 1916. Ueber das Altern einer Kolonie von *Syncoryne* und damit verbundene Knospungen am Hydrathenköpfchen. *Helgoländer wissenschaftliche Meeresuntersuchungen* 11: 91-125.
- HARTLAUB, C. 1917. Craspedote Medusen. Teil 1, Lief. 4, Williadae. *Nordisches Plankton* 6: 365-479.
- HAUENSCHILD, C. 1956. Experimentelle Untersuchungen über die Entstehung asexueller Klone bei der Hydromeduse *Eleutheria dichotoma*. *Zeitschrift für Naturforschung* 11: 394-402.
- HAUENSCHILD, C. 1957a. Ergänzende Mitteilung über die asexuellen Medusenklone bei *Eleutheria dichotoma*. *Zeitschrift für Naturforschung* 12B: 412-413.
- HAUENSCHILD, C. 1957b. Versuche über die Wanderung der Nesselzellen bei der Meduse *Eleutheria dichotoma*. *Zeitschrift für Naturforschung* 12B: 472-477.
- HEIP, C. 1971. The succession of benthic micrometazoans in a brackish water habitat. *Biologisch Jaarboek* 39: 191-196.
- HEIP, C. & SMOL, N. 1976. On the importance of *Protohydra leuckarti* as a predator of meio-benthic populations (pp. 285-296). In: PERSOONE, G. & JASPERS, E. (eds). Proceedings of the 10th European Marine Biology Symposium, volume 2, Population in dynamics of marine organisms in relation with nutrient cycling in shallow waters. *Universa Press, Wetteren, Belgium*, 710 pp.
- HEWITT, C. L. & GODDARD, J. H. R. 2001. A new species of large and highly contractile hydroid in the genus *Candelabrum* (Hydrozoa: Anthoathecatae) from southern Oregon, U.S.A. *Canadian Journal of Zoology* 79: 2280-2288.
- HICKSON, S. J. 1920. On the occurrence of *Protohydra* in England. *Quarterly Journal of Microscopic Science* 64: 419-424.
- HINCKS, T. 1861. On *Clavatella*, a new genus of corynoid polypes, and its reproduction. *Annals and Magazine of Natural History* (3)7: 73-81.
- HINCKS, T. 1868. A history of the British hydroid zoophytes. *John van Voorst, London*. Volume 1, pp. lxxvii +338 ; volume 2, 67 plates.
- HINCKS, T. 1872b. Contribution to the History of the Hydroida. *Annals and Magazine of Natural History ser. 4* 10: 385-395, pl. 20.
- HIRAI, E. 1958. On the species of *Cladonema radiatum* var. *mayeri* Perkins. *Bulletin of the Marine Biological Station of Asamushi, Tohoku University* 9: 23-25.



- HIROHITO, EMPEROR OF JAPAN 1977. Five hydroid species from the Gulf of Aqaba, Red Sea. *Biological Laboratory Imperial Household, Tokyo*, pp. 1-26, pls 1-3.
- HIROHITO, EMPEROR OF JAPAN 1988. The hydroids of Sagami Bay collected by His Majesty the Emperor of Japan. *Biological Laboratory of the Imperial Household, Tokyo*, pp. 179, 4 plates.
- HOTCHKISS, A. E., MARTIN, V. J. & APKARIAN, R. P. 1984. A scanning electron microscopic surface and cryofracture study of development in the planulae of the hydrozoan, *Pennaria tiarella*. *Scanning Electron Microscopy* 2: 717-727.
- HULT, J. 1941. Ueber einige für die Westküste Schwedens neue niedere Evertebraten. *Zoologiska Bidrag från Uppsala* 20: 455-460.
- HYMAN, L. H. 1947. Two new Hydromedusae from the Californian coast. *Transactions of the American microscopical Society* 66: 262-268.
- JÄDERHOLM, E. 1908. Die Hydroiden des sibirischen Eismeeress, gesammelt von der Russischen Polar-Expedition 1900-1903. *Mémoires de l'Académie des Sciences de St.-Petersbourg* 18: 1-26, plates.
- JÄDERHOLM, E. 1909. Northern and arctic invertebrates in the collection of the Swedish state museum (Riksmuseum). IV Hydroiden. *Bihang till Kungliga Svenska Vetenskaps-akademiens Handlingar* 45: 1-24.
- JARVIS, F. E. 1922. The hydroids from the Chagos, Seychelles and other islands and from the coasts of British East Africa and Zanzibar. *Transaction of the Linnean Society of London, Zoology* 18: 331-360, pls 24-26.
- JOHANNESSEN, G. 1924. *Monocoryne gigantea* (Bonnevie) Broch. *Skrifter Norske Videnskaps-akademi Matematisk Naturvidenskapelig Klasse* 1923(18): 1-9, pl. 1-2.
- JONES, N. S. 1950. Marine botton communities. *Biological reviews and biological proceedings of the Cambridge Philosophical Society* 25: 283-313.
- KEFERSTEIN, W. & EHLERS, E. 1861. Zoologische Beiträge gesammelt in Winter 1859-1860 in Neapel und Messina. *Leipzig*, pp. viii + 112, 15 plates.
- KEM, W. R. & OSTMAN, C. 1992. Occurrence of a hemolytic protein toxin in nematocysts of a marine benthic hydroid, *Halocordyle disticha* (Goldfuss). *Scientia Marina* 56: 193-203.
- KINGSLEY, J. S. 1910. A synopsis of the fixed hydroids of New England. *Tufts College Studies (Scientific Series)* 3: 13-38.
- KIRKENDALE, L. & CALDER, D. R. 2003. Hydroids (Cnidaria: Hydrozoa) from Guam and the Commonwealth of the Northern Marianas Islands (CNMI). *Micronesica* 36: 159-188.
- KIRKPATRICK, R. 1890. Reports on the zoological collections made in Torres Straits by Professor A. C. Haddon, 1888-1889. Hydroida and Polyzoa. *Proceedings of the Royal Dublin Society, n. s.* 6: 603-626.
- KOLLER, G. 1927. Ueber die geschlechtliche Fortpflanzung der *Protohydra leuckarti* Greeff. *Zoologischer Anzeiger* 73: 97-100.
- KOROTNEFF, A. DE 1888. Contribution à l'étude des Hydraires. *Archives de Zoologie Expérimentale et Générale* 6: 21-36, pls 1-2.
- KRAMP, P. L. 1930. Hydromedusae collected in the south-western part of the North Sea and in the eastern part of the Channel in 1903-14. *Mémoires du Musée royal d'histoire naturelle de Belgique* 45: 1-45.
- KRAMP, P. L. 1935. Polypdyr (Coelenterata) I. Ferskvandspolypper og Goplepolypper. *Danmarks Fauna* 41: 1-207.
- KRAMP, P. L. 1937. Polypdyr (Coelenterata), II. Gopler. *Danmarks Fauna* 43: 1-223.
- KRAMP, P. L. 1949. Origin of the hydroid family Corymorphidae. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i København* 111: 183-215.
- KRAMP, P. L. 1955. The medusae of the tropical West Coast of Africa. *Atlantide Report* 3: 239-324, pls 1-3.
- KRAMP, P. L. 1959. The Hydromedusae of the Atlantic Ocean and adjacent waters. *Dana Report* 46: 1-283.



- KRAMP, P. L. 1961. Synopsis of the medusae of the world. *Journal of the Marine Biological Association of the U. K.* 40: 1-469.
- KRAMP, P. L. 1968. The Hydromedusae of the Pacific and Indian Oceans. Sections II and III. *Dana Report* 72: 1-200.
- KRAMP, P. L. & DAMAS, D. 1925. Les Méduses de la Norvège. Introduction et partie spéciale. *Videnskabelige meddelelser fra Dansk naturhistorisk Forening* 80: 217-323.
- KROHN, A. 1853a. Ueber einige niedere Thiere. *Archiv für Anatomie, Physiologie und wissenschaftliche Medicin* 1853: 137-141.
- KROHN, A. 1853b. Ueber die Brut des *Cladonema radiatum* und deren Entwicklung zum Stauridium. *Archiv für Anatomie, Physiologie und wissenschaftliche Medicin* 1853: 420-426.
- KRUMBACH, T. 1907. Beiträge zur Kenntnis der Meduse *Eleutheria (Clavatella)* aus dem Golfe von Triest. PhD Thesis, printed by Wilhelm Gottlieb Korn, Breslau, pp. 47.
- KÜHL, H. 1962. Die Hydromedusen der Elbmündung. *Abhandlungen und Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg* 6: 209-232.
- KÜHL, H. 1967. Die Hydromedusen der Emsmündung. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven* 10: 239-246.
- KÜHL, H. 1971. Die Hydromedusen der Wesermündung. *Vie Milieu, suppl.* 22: 803-810.
- KÜHN, A. 1910. Die Entwicklung der Geschlechtsindividuen der Hydromedusen. Studien zur Ontogenese und Phylogenese der Hydroiden. II. *Zoologische Jahrbücher. Abteilung für Anatomie und Ontogenie der Tiere* 30: 43-174.
- KÜHN, A. 1913. Entwicklungsgeschichte und Verwandtschaftsbeziehungen der Hydrozoen. I. Teil: Die Hydroiden. *Ergebnisse und Fortschritte der Zoologie* 4: 1-284.
- KUHN, K., STREIT, B. & SCHIERWATER, B. 1996. Homeobox genes in the cnidarian *Eleutheria dichotoma*: evolutionary implications for the origin of Antennapedia-class (HOM/hox) genes. *Molecular Phylogenetics and Evolution* 6: 30-38.
- LEES, D. C. 1968. The addition of the hydroid *Cladocoryne floccosa* to the California marine fauna. *Bulletin of the Southern California Academy of Sciences* 67: 59-64.
- LEIDY, J. 1855. Contributions towards a knowledge of the marine invertebrate fauna, of the coasts of Rhode Island and New Jersey. *Journal of the Academy of Natural Sciences of Philadelphia, 2nd series* 3: 135-152.
- LELOUP, E. 1930. A propos de l'hydraire *Margelopsis haeckeli* Hartlaub. *Annales de la Société royale zoologique de Belgique* 60: 97-100.
- LELOUP, E. 1946. *Margelopsis haeckeli* Hartlaub, 1897, forme indicatrice du plancton au large de la côte belge. Contribution à l'étude de la faune belge, XV. *Bulletin du Musée royal d'histoire naturelle de Belgique* 22: 1-3.
- LELOUP, E. 1947. Les Coelentérés de la faune Belge. Leur bibliographie et leur distribution. *Mémoires du Musée royal d'histoire naturelle de Belgique* 107: 1-73.
- LENGERICH, H. 1922. Zur systematische Auffassung der Eleutheriiden. *Zoologischer Anzeiger* 54: 209-215.
- LENGERICH, H. 1923a. Vergleichende Morphologie der Eleutheriiden. Beiträge zur Kenntnis der Eleutheriiden II. *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere* 44: 311-388.
- LENGERICH, H. 1923b. Ektodermale Medusenknospung bei *Eleutheria radiata*. *Verhandlungen der deutschen zoologischen Gesellschaft* 28: 64-65.
- LESH-LAURIE, G. E. 1976. Stolon vs. hydranth determination in *Pennaria tiarella* planulae: a role for DNA synthesis (pp. 365-375). In: G.O. MACKIE (ed.). *Coelenterate Ecology and Behavior*. Plenum Press, New York & London, XIII, 744 pp.
- LUTHER, A. 1923. Ueber das Vorkommen von *Protohydra leuckarti* Greeff bei Tvärminne nebst komplettierenden Bemerkungen über den Bau dieses Polypen. *Acta Societatis pro fauna et flora Fennica* 52: 1-23.
- MADSEN, H. 1939. *Protohydra leuckarti* Greeff, neu für Dänemark. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i København* 103: 551-557.

- MAIER, E. M. 1974. Coelenterata. In: MORDUKHAI BOLTOVSKOGO, F.D. [Ed.] [Atlas of the Aral Sea invertebrates.]. *Pishchevaya Promyshlennost, Moscow*.
- MAMMEN, T. A. 1963. On a collection of hydroids from South India. I. Suborder Athecata. *Journal of the Marine biological Association of India* 5: 27-61.
- MANTON, S. M. 1941. On the hydrorhiza and claspers of the hydroid *Myriothele cocksi* (Vigurs). *Journal of the Marine Biological Association of the U. K.* 25: 143-150.
- MARCOCI, G. 1956. *Protohydra leuckarti* Greeff in apele teritoriale romineti ale Mrii Negre. *Protohydra leuckarti* Greeff dans les eaux roumaines de le Mer Noire. *Buletinul de cercetari piscicole* 15: 95-98.
- MARTIN, V. J. 1980. Nerve elements in the planula of the hydrozoan *Pennaria tiarella*. *Journal of Morphology* 166: 27-36.
- MARTIN, V. J. 1987. A morphological examination of gastrulation in a marine athecate hydrozoan. *Biological Bulletin* 173: 324-334.
- MARTIN, V. J. 1988a. Development of nerve cells in hydrozoan planulae: 1. Differentiation of ganglionic cells. *Biological Bulletin* 174: 319-329.
- MARTIN, V. J. 1988b. Development of nerve cells in hydrozoan planulae: 2. Examination of sensory cell differentiation using electron microscopy and immunocytochemistry. *Biological Bulletin* 175: 65-78.
- MARTIN, V. J. 1990. Development of nerve cells in hydrozoan planulae: 3. Some interstitial cells traverse the ganglionic pathway in the endoderm. *Biological Bulletin* 178: 10-20.
- MARTIN, V. J. 1991. Differentiation of the interstitial cell line in hydrozoan planulae 1. Repopulation of epithelial planulae. *Hydrobiologia*
- MARTIN, V. J. 1992a. Characterization of a RFamide-positive subset of ganglionic cells in the hydrozoan planular nerve net. *Cell And Tissue Research* 269: 431-438.
- MARTIN, V. J. 1992b. Characterization of a RFamide-positive subset of ganglionic cells in the hydrozoan planular nerve net. *Cell And Tissue Research* 269: 431-438.
- MARTIN, V. J. 2000. Reorganization of the nervous system during metamorphosis of a hydrozoan planula. *Invertebrate Biology* 119: 243-253.
- MARTIN, V. J., & ARCHER, W. E. 1986a. A scanning electron microscopic study of embryonic development of a marine hydrozoan. *Biological Bulletin of the Marine Biological Laboratory, Woods Hole* 171: 116-125.
- MARTIN, V. J., & ARCHER, W. E. 1986b. Migration of interstitial cells and their derivatives in a hydrozoan planula. *Developmental Biology* 116: 486-496.
- MARTIN, V. J., & ARCHER, W. E. 1997. Stages of larval development and stem cell population changes during metamorphosis of a hydrozoan planula. *Biological Bulletin* 192: 41-52.
- MARTIN, V. J., & THOMAS, M. B. 1977. A fine structural study of embryonic and larval development in the gymnoblastic hydroid *Pennaria tiarella*. *Biological Bulletin of the Marine Biological Laboratory, Woods Hole* 153: 198-218.
- MARTIN, V. J., & THOMAS, M. B. 1981a. Elimination of the interstitial cells in the planula larva of the marine hydrozoan *Pennaria tiarella*. *Journal of Experimental Zoology* 217: 303-323.
- MARTIN, V. J., & THOMAS, M. B. 1981b. The origin of the nervous system in *Pennaria tiarella*, as revealed by treatment with colchicine. *Biological Bulletin* 160: 303-310.
- MARTIN, V. J., & THOMAS, M. B. 1983. Establishment and maintenance of morphological polarity in epithelial planulae. *Transactions of the American Microscopical Society* 102: 18-24.
- MARTIN, V. J. & THOMAS, M. B. 1977. A fine structural study of embryonic and larval development in the gymnoblastic hydroid *Pennaria tiarella*. *Biological Bulletin of the Marine Biological Laboratory, Woods Hole* 153: 198-218.
- MAYER, A. G. 1904. Medusae of the Bahamas. *Memoirs of Natural Sciences / Museum of the Brooklyn Institute of Arts and Sciences* 1: 1-33, pls 1-7.
- MAYER, A. G. 1910. Medusae of the world. Hydromedusae, Vols. I & II. Scyphomedusae, Vol III. *Carnegie Institution, Washington*, pp. 735, plates 1-76.

- MCCRADY, J. 1859. Gymnophthalmata of Charleston Harbor. *Proceedings of the Elliott Society of Natural History* 1: 103-221.
- MEDEL, D., & LOPEZ GONZALEZ, P. J. 1996. Updated catalogue of hydrozoans of the Iberian Peninsula and Balearic Islands, with remarks on zoogeography and affinities. *Scientia Marina* 60: 183-209.
- MIGOTTO, A. E. 1996. Benthic shallow-water hydroids (Cnidaria, Hydrozoa) of the coast of São Sebastião, Brazil, including a checklist of Brazilian hydroids. *Zoologische Verhandelingen, Leiden* 306: 1-125.
- MILLARD, N. A. H. 1966. The Hydrozoa of the south and west coasts of South Africa. Part III. The Gymnoblastera and small families of the Calyptoblastea. *Annals of the South African Museum* 48: 427-487, pl. 1.
- MILLARD, N. A. H. 1975. Monograph on the Hydroida of southern Africa. *Annals of the South African Museum* 68: 1-513.
- MILLARD, N. A. H. & BOUILLON, J. 1973. Hydroids from the Seychelles (Coelenterata). *Annales du Musée Royal de l'Afrique Centrale, Sciences Zoologiques* 206: 1-106, pls 1-5.
- MILLARD, N. A. H. & BOUILLON, J. 1974. A collection of hydroids from Mocambique, East Africa. *Annals of the South African Museum* 65: 1-40.
- MONNIOT, F. 1962. Recherches sur les graviers à *Amphioxus* de la région de Banyuls-sur-Mer. *Vie et Milieu* 13: 231-322.
- MORRI, C. & BIANCHI, C. N. 1999. Hydroids (Cnidaria: Hydrozoa) from the Aegean Sea, mostly epiphytic on algae. *Cahiers de Biologie Marine* 40: 283-291.
- MORRI, C. & BOERO, F. 1986. Volume 7. Hydroids. *Office d'Etudes Marines et Atmosphériques, Bruxelles*, 91 pp.
- MOTZ-KOSSOWSKA, S. 1905. Contribution à la connaissance des hydraires de la Méditerranée occidentale. I. Hydraires gymnoblastiques. *Archives de Zoologie Expérimentale et Générale* (4)3: 39-98, pl. 3.
- MÜLLER, H. 1908. Untersuchungen über Eibildung bei Cladonemiden und Codoniden. *Zeitschrift für wissenschaftliche Zoologie* 89: 28-80, pls 3-5.
- MÜLLER, H. 1911. Beiträge zur Kenntnis der Gattung *Eleutheria*. *Archiv für Naturgeschichte* 77, suppl. 1: 159-169, pl. 3.
- MUUS, K. 1966. Notes on the biology of *Protohydra leuckarti* Greef (Hydroidea, Protohydrae). *Ophelia* 3: 141-150.
- NAUMOV, D. V. 1955a. Tip Kishetsnopolostnie-Coelenterata (pp. 51-68, pls. 7-9). In: USHAKOV, P.V. et al. (eds). Atlas bespozvonochnikh dal'nevostochnikh morei SSSR. *Akademii Nauk SSSR, Moscow & Leningrad*, 244 pp., 66 leaves of pls.
- NAUMOV, D. V. 1969. Hydroids and Hydromedusae of the USSR. *Israel Program for scientific translation, Jerusalem*, 463 pp., 30 plates.
- NYHOLM, K. G. 1951a. A contribution to the study of the sexual phase of *Protohydra leuckarti*. *Arkiv för Zoologi* 2: 529-530, plate.
- NYHOLM, K. G. 1951b. Egg cells in the ectoderm of *Boreohydra simplex*. *Arkiv för Zoologi* 2: 531-533.
- ÖSTMAN, C., PIRAINO, S. & KEM, W. 1991. Nematocysts of the Mediterranean hydroid *Halcordyle disticha*. *Hydrobiologia* 216-217: 607-613.
- OMER-COOPER, J. 1964. On *Protohydra psamathe* n. sp. from South Africa. *Journal of the Linnean Society, London, Zoology* 45: 145-150.
- PARDY, R. L. & LENHOFF, H. M. 1968. The feeding biology of the gymnoblastic hydroid, *Pennaria tiarella*. *Journal of experimental Zoology* 168: 197-202.
- PASTEELS, J. 1939. Variations et gradient axial chez l'hydroméduse *Cladonema radiatum*. *Annales de la Société royale zoologique de Belgique* 69: 311-325.
- PASTEELS, J. 1941. Régénération de l'hydranthe et de la méduse chez *Cladonema radiatum*. *Annales de la Société royale zoologique de Belgique* 72: 63-73.
- PEÑA CANTERO, A. L. & GARCIA CARRASCOSA, A. M. 2002. The benthic hydroid fauna of the Chafarinas Islands (Alboran Sea, western Mediterranean). *Zoologische Verhandelingen* 337: 1-180.



- PERKINS, H. F. 1902. Notes on the anatomy and histology of a new form of *Cladonema* from the Bahamas. *Johns Hopkins University Circulars* 21: 25-27, pl. 1.
- PERRIER, E. 1886. Les explorations sous-marines. *Hachette, Paris*, pp. 352.
- PETERSEN, C. G. J. 1913. Valuation of the sea. II The animal communities of the sea bottom and their importance for marine zoogeography. *Report for the Danish Biological Station* 21: 1-42.
- PETERSEN, K. W. 1990. Evolution and taxonomy in capitate hydroids and medusae (Cnidaria: Hydrozoa). *Zoological Journal of the Linnean Society* 100: 101-231.
- PHILBERT, M. 1936. Etudes sur *Cladocoryne floccosa* Rotch. *Bulletin de l'Institut océanographique de Monaco* 708: 1-16.
- PICARD, J. 1957. Etude sur les hydroides de la superfamille Pteronematoidea, 1. Généralités. *Bulletin de l'Institut océanographique de Monaco* 1106: 1-12.
- PICARD, J. 1958. Notes sur une collection d'hydroides provenant des côtes méditerranéennes d'Israel. *Bulletin of the Sea Fisheries Research Station, Israel* 15: 1-3.
- PICTET, C. 1893. Etude sur les hydraires de la Baie d'Amboine. *Revue suisse de Zoologie* 1: 1-64.
- POCHE, F. 1914. Das System der Coelenterata. *Archive für Naturgeschichte* 80: 47-128.
- PRÉVOT, E. 1959. Morphologie et évolution des structures tentaculaires chez les hydraires gymnoblastes Capitata. *Recueil des Travaux de la station marine d'Endoume* 29: 91-128.
- QUATREFAGES, A. DE 1842a. Mémoire sur l'Eleutherie dichotome (*Eleutheria dichotoma* nob.), nouveau genre de Rayonnés, voisin des Hydres. *Annales des Sciences naturelles* (2)18: 270-288, plate 8.
- QUATREFAGES, A. DE 1842b. Mémoire sur l'Eleutherie dichotome (*Eleutheria dichotoma* A. de Q.). Nouveau genre de Rayonnés, voisin des Hydres. *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences, Paris* 15: 168-170.
- RALPH, P. M. 1953. A guide to the athecate (Gymnoblatic) hydroids and medusae of New Zealand. *Tuatara* 5: 59-75.
- RASMUSSEN, E. 1973. Systematics and ecology of the Isefjord marine fauna (Denmark). With a survey of the eelgrass (*Zostera*) vegetations and its communities. *Ophelia* 11: 1-495.
- REES, W. J. 1941. Notes on British and Norwegian hydroids and medusae. *Journal of the Marine Biological Association of the United Kingdom* 25: 129-141.
- REES, W. J. 1949. On *Cladonema myersi*, a new species of hydroid from the Californian coast. *Proceedings of the Zoological Society of London* 119: 861-865.
- REES, W. J. 1956. A revision of some northern gymnoblatic hydroids in the Zoological Museum, Oslo. *Nytt Magasin for Zoologi* 4: 109-120.
- REES, W. J. 1957. Evolutionary trends in the classification of capitate hydroids and medusae. *Bulletin of the British Museum (Natural History)*. *Zoology series* 4: 455-534.
- REES, W. J. 1958. The status of the hydroid *Symplectanea bracteata* Fraser. *Nytt magasin för Zoologi* 5: 17-19.
- REES, W. J. & THURSFIELD, S. 1965. The hydroid collections of James Ritchie. *Proceedings of the Royal Society of Edinburgh (B)* 69: 34-220.
- REES, J. T. 1979. The polyp and immature medusa stages of *Cladonema californicum*, Hyman, 1947 (Anthomedusae: Cladonemidae) with biological notes and a discussion of the taxonomy of the genus *Cladonema*. *Journal of Natural History* 13: 295-302.
- RICHTERS, F. 1908. *Cladonema radiatum* bei Helgoland. *Zoologischer Anzeiger* 33: 687.
- RIEDL, R. 1970. Fauna und Flora der Adria, ed. 2: 1-640, col. pls 1-8, pls 1-235, figs. Verlag Paul Parey, Hamburg & Berlin.
- RITCHIE, J. 1910. The marine fauna of the Mergui Archipelago, lower Burma etc.- the Hydroids. *Proceedings of the Zoological Society of London* 1910: 799-825, plates.
- ROTCH, W. D. 1871. On a new genus and species of Hydroid Zoophytes (*Cladocoryne floccosa*). *Annals and Magazine of Natural History* (4) 7: 227-228.



- RUEBUSH, T. K. 1939. The occurrence of the two rare genera, *Protohydra* and *Protodrilus* on the East coast of North America. *Science*, N.Y. 90: 617-618.
- RUSSELL, F. S. 1953. The medusae of the British Isles. *Cambridge University Press, London*, pp. 530, 35 pls.
- SALVINI-PLAWEN, L. v. 1966. Zur Kenntnis der Cnidaria des nordadriatischen Mesopsammon. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven, Sonderband 2*: 165-186.
- SARS, G. O. 1874. Bidrag til Kundskaben om Norges Hydroider. *Forhandlinger i Videnskabs-Selskabet i Kristiana* (1873): 91-150, pls 2-5.
- SARS, M. 1850. Beretning om en i sommeren 1849 foretagen zoologisk reise i Lofoten og Finnmarken. *Christina*, 91 pp.
- SARS, M. 1874. In: SARS, G. O. 1874.
- SARS, M. 1877. Nye og mindre bekjendte Coelenterater. - New and little known Coelenterates (pp. 32, pls 1-2). In: J. KOREN & D. C. DANIELSSEN (eds). *Fauna littoralis Norvegiae* Bergen.
- SCHOURING, L. 1922. Die Hydroiden. Untersuchungsfahrt des Reichsforschungsdampfer "Poseidon" in das Barentsmeer im Juni und Juli 1913. *Wissenschaftliche Meeresuntersuchungen. Abt. Helgoland*. 13: 157-179.
- SCHIERWATER, B. 1989. Allometric changes during growth and reproduction in *Eleuthera dichotoma* (Hydrozoa, Athecata) and the problem of estimating body size in a microscopic animal. *Journal of Morphology* 200: 255-267.
- SCHIERWATER, B. & HADRY, H. 1998. Environmental factors and metagenesis in the hydroid *Eleuthera dichotoma*. *Invertebrate Reproduction and Development* 34: 139-148.
- SCHIERWATER, B. & HAVENSCHILD, C. 1990. The position and consequences of a vegetative mode of reproduction in the life cycle of a hydromedusa and an oligochaete worm. *Advances In Invertebrate Reproduction* 5: 37-42.
- SCHIERWATER, B., MURTHA, M., DICK, M., RUDDLE, F. H. & BUSS, L. W. 1991. Homeoboxes in cnidarians. *Journal of Experimental Zoology* 260: 413-416.
- SCHIERWATER, B., PIEKOS, B. & BUSS, L. W. 1992. Hydroid stolonal contractions mediated by contractile vacuoles. *Journal of Experimental Biology* 162: 1-21.
- SCHMIDT, O. 1869. Leben der Krebse, Würmer und ungegliederte Wirbellosen Thiere. In: BREHM, A.E. *Illustriertes Thierleben. Hildburghausen*. 6 volumes.
- SCHNEIDER, G. 1927. Neue Fundorte für *Protohydra leuckarti* Greeff bei der zoologischen Station Tvärminne. *Memoranda Societatis pro Fauna Flora Fennica* 2: 8-10.
- SCHÖNBORN, C., ARNDT, E. A. & GOSSELCK, F. 1993. Bestimmungsschlüssel der benthischen Hydrozoen der Ostsee. *Mitteilungen aus dem Zoologischen Museum in Berlin* 69: 201-253.
- SCHUCHERT, P. 1996. The marine fauna of New Zealand: athecate hydroids and their medusae (Cnidaria: Hydrozoa). *New Zealand Oceanographic Institute Memoir* 106: 1-159.
- SCHUCHERT, P. 2000. Hydrozoa (Cnidaria) of Iceland collected by the BIOICE programme. *Sarsia* 85: 411-438.
- SCHUCHERT, P. 2001a. Hydroids of Greenland and Iceland (Cnidaria, Hydrozoa). *Meddelelser om Grønland, Bioscience* 53: 1-184.
- SCHUCHERT, P. 2001b. Survey of the family Corynidae (Cnidaria, Hydrozoa). *Revue suisse de Zoologie* 108: 739-878.
- SCHUCHERT, P. 2003. Hydroids (Cnidaria, Hydrozoa) of the Danish expedition to the Kei Islands. *Steenstrupia* 27: 137-256.
- SCHUCHERT, P. 2004. Revision of the European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Families Oceanidae and Pachycordylidae. *Revue suisse de Zoologie* 111: 315-369.
- SCHUCHERT, P. 2005. Species boundaries in the hydrozoan genus *Coryne*. *Molecular Phylogenetics and Evolution* 36: 194-199.

- SCHULZ, E. 1950a. Zur Oekologie von *Protohydra leuckarti* Greef. (Studien an Hydrozoa, I.). *Kieler Meeresforschung* 7: 53-57.
- SCHULZ, E. 1950b. *Psammohydra nanna*, ein neues solitäres Hydrozoon in der westlichen Beltsee. (Studien an Hydrozoa, II). *Kieler Meeresforschung* 7: 122-137.
- SCHULZ, E. 1952. Ungeschlechtliche Fortpflanzung durch Knospung bei *Protohydra leuckarti* Greef (Studien an Hydrozoa, III). *Kieler Meeresforschung* 7: 68-69.
- SCHULZE, F. E. 1876. *Tiarella singularis*, ein neuer Hydroidpolyp. *Zeitschrift für wissenschaftliche Zoologie* 27: 403-416.
- SEGONZAC, M. & VERVOORT, W. 1995. First record of the genus *Candelabrum* (Cnidaria, Hydrozoa, Athecata) from the Mid-Atlantic Ridge: a description of a new species and a review of the genus. *Bulletin du Muséum national d'histoire naturelle. Section A, Zoologie, biologie et écologie animales* 17: 31-63.
- SEGERSTEDT, M. 1889. Bidrag till Kännedom om Hydroid-Faunan vid Sveriges Vestkust. *Bihang till Kungliga Svenska Vetenskaps-akademiens Handlingar* 14(4): 1-28, plate.
- SPAGNOLINI, A. 1876. Catalogo sistematico degli Acalefi del Mediterraneo. Sifonofori e Meduse Craspedote. *Atti della Società italiana di scienze naturali* 19: 291-333.
- SPRACKLIN, B. W. 1982. Hydroidea (Cnidaria: Hydrozoa) from Carrie Bow Cay, Belize. *Smithsonian Contribution to Marine Science* 12: 239-251.
- STECHOW, E. 1909. Hydroidpolypen der japanischen Ostküste. I. Teil: Athecata und Plumularidae. In: DOFLEIN, F. (ed.). Beiträge zur Naturgeschichte Ostasiens. *Abhandlungen der Mathematisch-Physikalische Klasse der Königlich Bayerischen Akademie der Wissenschaften, Supplement Band 1*: 1-111, plates 1-7.
- STECHOW, E. 1919. Zur Kenntnis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete, nebst Angaben über einige Kirchenpauer'sche Typen von Plumulariden. *Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere* 42: 1-172.
- STECHOW, E. 1920. Neue Ergebnisse auf dem Gebiete der Hydroidenforschung. *Sitzungsberichte der Gesellschaft für Morphologie und Physiologie in München* 31: 9-45.
- STECHOW, E. 1921. Neue Genera und Species von Hydrozoen und anderen Evertibraten. *Archiv für Naturgeschichte* 87: 248-265.
- STECHOW, E. 1923. Zur Kenntnis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete. II. Teil. *Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere* 47: 29-270.
- STECHOW, E. 1925. Hydroiden von West- und Südwestaustralien nach den Sammlungen von Prof. Dr. Michaelsen und Prof. Dr. Hartmeyer. *Zoologische Jahrbücher. Abteilung für Systematik, Oekologie und Geographie der Tiere* 50: 191-270.
- STEPANJANTS, S. D., SHEIKO, O. V. & NÄPARA, T. O. 1990. *Fabulosus kurilensis* gen. et sp. n. (Hydrozoa, Chidaria [Cnidaria]), a new hydroid [hydroid] polyp of the Kuril Islands shelf. *Trudy Zoologicheskogo Instituta* 218: 5-17.
- STEPANJANTS, S. D., OVANESYAN, I. G. & SIRENKO, B. I. 1993. Cladonematidae representative (Hydrozoa, Athecata, Capitata) in Saint-Petersburg aquariums. *Cladonema* revision [Russian with English summary]. *Issledovaniya Fauny Morei* 45: 90-105.
- STEPANJANTS, S. D., CHRISTIANSEN, B. O., SVOBODA, A. & ANOKHIN, B. A. 2003. The genus *Monocoryne* (Hydrozoa, Capitata): peculiarities of morphology, species composition, biology and distribution. *Sarsia* 88: 97-106.
- STIMPSON, W. 1854. Synopsis of the marine Invertebrata of Grand Manan, or the region about the mouth of the Bay of Fundy, New Brunswick. *Smithsonian Contributions to Knowledge* 6: 1-67, pls 1-3.
- SUMMERS, R. G. 1970. The fine structure of the spermatozoa of *Pennaria tiarella* (Coelenterata). *Journal of Morphology* 131: 117-130.
- SUMMERS, R. G., & HAYNES, J. F. 1969. The ontogeny of interstitial cells in *Pennaria tiarella*. *Journal of Morphology* 129: 81-87.

- SUMMERS, R. S. 1976. An ultrastructural investigation of the striated subumbrellar structure of the Anthomedusan, *Pennaria tiarella*. *Journal of Morphology* 149: 507-525.
- SUMMERS, R. G. & HAYNES, J. F. 1969. The ontogeny of interstitial cells in *Pennaria tiarella*. *Journal of Morphology* 129: 81-87.
- SWEDMARK, B. 1956. Étude de la microfaune des sables marins de la région de Marseille. *Archives de Zoologie expérimentale et générale*, 93, notes et revue 2: 70-95.
- SWEDMARK, B. 1959. On the biology of sexual reproduction of the interstitial fauna of marine sand. *Proceedings of the XV International Congress of Zoology*, 327-330.
- SWENANDER, G. 1904. Ueber die Athecaten Hydroiden des Drontheimsfjordes. *Kongelige Norske Videnskabers Selskab Skrifter* 1903: 1-16, pl. 1.
- SWOFFORD, D. L. 2001. PAUP\*. Phylogenetic Analysis Using Parsimony (\*and Other Methods). Version 4. *Sinauer Associates, Sunderland, Massachusetts*.
- TARDENT, P. 1963. Regeneration in the Hydrozoa. *Biological Reviews* 38: 293-333.
- TARDENT, P. 1965. Developmental aspects of regeneration in Coelenterates (pp. 71-88). In: KIORTIS, V. & TRAMPUSCH, H.A.L. (eds). *Regeneration in Animals and related problems. North-Holland Press, Amsterdam*.
- TARDENT, P. 1978. Coelenterata, Cnidaria (pp. 71-415). In: SEIDEL, F. (ed). *Morphogenese der Tiere. Gustav Fischer, Stuttgart*.
- TARDENT, P. & STÖSSEL, F. 1971. Die Mechanoreceptoren der Polypen von *Coryne pintneri*, *Sarsia reesi* und *Cladonema radiatum* (Athecata, Capitata). *Revue suisse de Zoologie* 78: 680-688.
- TEISSIER, G. 1965. Inventaire de la faune marine de Roscoff. Cnidaires-Cténaires. *Travaux de la Station Biologique de Roscoff* 16: 1-53.
- THIEL, M. E. 1938. Die Leptolinae der "Meteor" Expedition in systematischer Betrachtung (I. Anthomedusae). *Zoologischer Anzeiger* 121: 289-303.
- THIEL, M. E. 1935. Zur Kenntnis der Hydromedusenfauna des Schwarzen Meeres. *Zoologischer Anzeiger* 111: 161-174.
- THIEL, H. 1988. Cnidaria (pp. 266-272). In: HIGGINS, R. P. & THIEL, H. (eds). *Introduction to the study of meiofauna. Smithsonian Institution Press, Washington, USA*.
- THOMAS, M. B., EDWARDS, N. C. & NORRIS, T. A. 1987. Gastrulation in *Halocordyle disticha* (Hydrozoa, Athecata). *International Journal of Invertebrate Reproduction And Development* 12: 91-102.
- THOMAS, M. B., EDWARDS, N. C. & HIGGINS, R. P. 1995. *Cryptohydra thieli* n. gen., n. sp.: a meiofaunal marine hydroid (Hydrozoa, Athecata, Capitata). *Invertebrate Biology* 114: 107-118.
- TOTTON, A. K. 1965. A synopsis of the Siphonophora. *British Museum (Natural History), London*, 230 pp.
- UCHIDA, T. 1924. On a new pelagic Hydroid, *Climacocodon ikarii* n. gen. n. sp. *Japanese Journal of Zoology* 1: 59-65.
- UCHIDA, T. 1927. Studies on Japanese hydromedusae. I. Anthomedusae. *Journal of the Faculty of Science, Imperial University of Tokyo, Section IV, Zoology* 1: 145-241, plates 10-11.
- VALKANOV, A. 1947. *Protohydra leuckarti* Greeff ot Chernomorska Biologichna Stantsiya (Arbeiten aus der Biologischen Meeresstation am Schwarzen Meer in Varna) 13: 31-35.
- VAN BENEDEN, P. J. 1867. Recherches sur la faune littorale de Belgique (polypes). *Mémoires de l'Académie Royale des Sciences et Belles-Lettres de Belgique* 36: 1-207.
- VEVERS, H. G. 1959. Birth of a *Tricyclusa*. *New Scientist* 6: 506-507.
- VAN DE VYVER, G. 1968. Etude du développement embryonnaire des hydraires athécates (Gymnoblastiques) à gonophores. 2. Formes à actinulas. *Archives de Biologie* 79: 327-363.
- VAN DE VYVER, G. & BOUILLON J. 1969. Etude du développement embryonnaire et de l'histogenèse de *Eleutheria dichotoma* (De Quatrefages) (Anthoméduse Eleutheriidae). *Annales d'embryologie et de morphogenèse* 2: 317-327.



- VERRILL, A. E. 1878. Notice of recent additions to the marine fauna of the eastern coast of North America. No. 2. Brief contributions to zoology from the Museum of Yale College. No. 39. *American Journal of Science* (3)16: 371-378.
- VERVOORT, W. 1946. Hydrozoa (C 1) A. Hydropolypen. *Fauna van Nederland* 14: 1-336.
- VERVOORT, W. 1968. Report on a collection of Hydroida from the Caribbean region, including an annotated checklist of Caribbean hydroids. *Zoologische Verhandelingen, Leiden* 92: 1-124.
- VERVOORT, W. 1993. Report on hydroids (Hydrozoa, Cnidaria) in the collection of the Zoological Museum, University of Tel-Aviv, Israel. *Zoologische Mededelingen* 67: 537-565.
- VERWOORT, W. V. 1985. Deep-water hydroids (pp. 267-297). In: LAUBIER, L. & MONNIOT, C. (eds). *Peuplements profonds du golfe de Gascogne: Campagnes BIOGAS. [Deep sea populations from the Gulf of Gascogne: BIOGAS expeditions.]* Ifremer, Brest, 629 pp. [incorrect spelling of name]
- VIGURS 1849/1850. In: COCKS, W. P. Contributions to the fauna of Falmouth. *Report of the Royal Cornwall Polytechnic Society* 17: 90. [publication date unclear, likely 1850, see Cornelius (1977)]
- WATSON, J. E. 1999. Hydroids (Hydrozoa: Anthoathecata) from the Beagle Gulf and Darwin Harbour, northern Australia. *The Beagle, Records of the Museums and Art Galleries of the Northern Territory* 15: 1-21.
- WEBER, C. 1980. Structural organization, ontogeny and regeneration of the eye of *Cladonema radiatum* (Anthomedusae) (pp. 347-352). In: TARDENT, P. & TARDENT, R. (eds). *Developmental and cellular biology of coelenterates. Proceedings of the 4th International Coelenterate Conference, Interlaken, Switzerland. Elsevier/Biomedical Press, Amsterdam, New York & Oxford*, pp. 499.
- WEBER, C. 1981a. Lens of the hydromedusan *Cladonema* studied by SDSgel-Electrophoresis and immunofluorescent technique. *Journal of Experimental Zoology* 217: 15-21.
- WEBER, C. 1981b. Structure, histochemistry, ontogenetic development, and regeneration of the ocellus of *Cladonema radiatum* Dujardin (Cnidaria, Hydrozoa, Anthomedusae). *Journal of Morphology* 167: 313-331.
- WEBER, C. & TARDENT, P. 1978. Zur Entwicklung des Linsenauges von *Cladonema radiatum* Duj. (Hydrozoa, Anthomedusae). *Revue suisse de Zoologie* 85: 762-767.
- WEDLER, E. & LARSON, R. 1986. Athecate hydroids from Puerto Rico and the Virgin Islands. *Studies on Neotropical Fauna and Environment* 21: 69-101.
- WEHLING, W. 1978. Observations on the reproductive biology of *Protohydra leuckarti*. *American Zoologist* 18: 643.
- WEILER-STOLT, B. 1960. Ueber die Bedeutung der interstitiellen Zellen für die Entwicklung und Fortpflanzung mariner Hydroiden. *Wilhelm Roux' Archiv* 152: 398-455.
- WEILL, R. 1931. Le genre *Pteroclava* n. gen., l'interprétation systématique des Ptéronemidae (Hydriaires) et la valeur taxonomique du cnidome. *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences, Paris* 192(2): 60-62.
- WEILL, R. 1934. Contribution à l'étude des Cnidaire et de leurs nématocystes. II. Valeur taxonomique du cnidome. *Travaux de la Station zoologique de Wimereux* 11: 349-701.
- WEILL, R. 1935. *Halammohydra* Remane, genre d'hydrozoaires aberrant. Son cnidome et sa position taxonomique: Affinités avec les Siphonophores Chondrophorides et avec *Protohydra Leuckarti* Greeff. *Bulletin de la Société Zoologique de France* 60: 73-87.
- WEILL, R. 1936. Le cnidome des Cladonémides *Eleutheria dichotoma* et *Cladonema radiatum*, son cycle et son interprétation. *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences, Paris* 203: 816-818.
- WEILL, R. 1937. Existence d'un monocnidome dans le médusoïde d'un polype (*Pennaria? tiarella* McCr) à tétracnidome. *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences, Paris* 204: 1749-1752.
- WEISMANN, A. 1883. Die Entstehung der Sexualzellen bei den Hydromedusen. Zugleich ein Beitrag zur Kenntnis des Baues und der Lebensgeschichte dieser Gruppe. *Gustav Fischer, Jena*, pp. 295.

- WERNER, B. 1954. Ueber die Fortpflanzung der Anthomeduse *Margelopsis haeckeli* Hartlaub durch Subitan- und Dauereier und die Abhängigkeit ihrer Bildung von äusseren Faktoren. *Verhandlungen der Deutschen Zoologischen Gesellschaft in Tübingen* 1954: 124-133.
- WERNER, B. 1955. On the development and reproduction of the Anthomedusan *Margelopsis haeckeli* Hartlaub. *Annals of the New York Academy of Sciences* 62: 1-30.
- WERNER, B. 1956. Der zytologische Nachweis der parthogenetischen Entwicklung bei der Anthomeduse *Margelopsis haeckeli* Hartlaub. *Naturwissenschaften* 43: 541-542.
- WESTBLAD, E. 1930a. *Protohydra Leuckarti* an der Swedischen Küste entdeckt. *Arkiv för Zoologi* 21: 1-4.
- WESTBLAD, E. 1930b. Ueber die Geschlechtsorgane und die systematische Bedeutung von *Protohydra Leuckarti* Greeff. *Arkiv för Zoologi* 21: 1-13.
- WESTBLAD, E. 1935. Neue Beobachtungen über *Protohydra*. *Zoologischer Anzeiger* 111: 152-158.
- WESTBLAD, E. 1937. *Boreohydra simplex* n. gen., n. sp., ein Solitärpolyp von der norwegischen Küste. *Arkiv för Zoologi* 29: 1-6.
- WESTBLAD, E. 1947. Notes on hydroids. *Arkiv för Zoologi* 39: 1-23.
- WESTBLAD, E. 1953. *Boreohydra simplex* Westblad, a "bipolar" hydroid. *Arkiv for Zoologi, new series* 4: 351-354.
- WIESER, W. 1958. Occurrence of *Protohydra leuckarti* in Puget Sound. *Pacific Science* 12: 106-108.
- WILL, L. 1913. *Acaulis primarius* Stimpson, ein neuer Ostsee Bewohner. *Sitzungsberichte und Abhandlungen der naturforschenden Gesellschaft zu Rostock, neue Serie* 5: 57-62.
- WIRTZ, P. & DEBELIUS, H. 2003. Mediterranean and Atlantic Invertebrate Guide. *ConchBooks, Hackenheim, Germany*, pp. 1-305.

## INDEX

- |  |   |
|--|---|
| <i>Acanthella</i> , 341                      | <i>cocksii</i> , <i>Candelabrum</i> , 341     |
| Acaulidae, 326                               | <i>corynaria</i> , <i>Hydra</i> , 370         |
| <i>Acaulis</i> , 328                         | Corynidae, 380                                |
| <i>Acauloides</i> , 330                      | <i>Dendronema</i> , 391                       |
| <i>Allmani</i> , <i>Cladonema</i> , 376      | Dendronemidae, 371                            |
| <i>ammisatum</i> , <i>Acauloides</i> , 330   | <i>dichobdella</i> , <i>Eleutheria</i> , 381  |
| <i>anisonema</i> , <i>Eleutheria</i> , 381   | <i>dichocnida</i> , <i>Eleutheria</i> , 381   |
| <i>Arum</i> , 341                            | <i>dichotoma</i> , <i>Eleutheria</i> , 381    |
| <i>Blastothela</i> , 328                     | <i>diplonema</i> , <i>Eleutheria</i> , 384    |
| <i>Boreohydra</i> , 334                      | <i>disticha</i> , <i>Pennaria</i> , 364       |
| Boreohydridae, 334                           | <i>Dujardinii</i> , <i>Cladonema</i> , 376    |
| <i>californicum</i> , <i>Cladonema</i> , 379 | <i>Eleutheria</i> , 380                       |
| Candelabridae, 340                           | Eleutheriidae, 371                            |
| <i>Candelabrum</i> , 341                     | <i>Eucoryne</i> , 364                         |
| <i>Cladocoryne</i> , 368                     | <i>floccosa</i> , <i>Cladocoryne</i> , 368    |
| Cladocorynidae, 368                          | <i>fritchmanii</i> , <i>Candelabrum</i> , 346 |
| <i>Cladocorynopsis</i> , 368                 | <i>Gegenbauri</i> , <i>Cladonema</i> , 376    |
| <i>Cladonema</i> , 375                       | <i>gemma</i> , <i>Eleutheria</i> , 381        |
| <i>cladonema</i> , <i>Stauridium</i> , 376   | <i>gigantea</i> , <i>Monocoryne</i> , 381     |
| Cladonematidae, 371                          | <i>Globiceps</i> , 364                        |
| <i>claparedei</i> , <i>Eleutheria</i> , 384  | <i>haeckelii</i> , <i>Margelopsis</i> , 356   |
| <i>claparedii</i> , <i>Eleutheria</i> , 384  | <i>Halocordyle</i> , 364                      |
| <i>Clavatella</i> , 380                      | <i>Halocordyle disticha</i> , 364, 367        |
| <i>Climacocodon</i> , 356                    | Halocordylidae, 363                           |
| <i>cnidobdella</i> , <i>Eleutheria</i> , 381 | <i>hartlaubii</i> , <i>Margelopsis</i> , 361  |
| <i>Cnidonema</i> , 373                       | <i>helleri</i> , <i>Polycoryne</i> , 370      |

- heptanema*, *Eleutheria*, 381  
*Herpusa*, 380  
*heteroclada*, *Eleutheria*, 381  
*heteronema*, *Eleutheria*, 384  
*hexanema*, *Eleutheria*, 381  
*Hydra corynaria*, 370  
*ilonae*, *Acauloides*, 332  
*krohni*, *Eleutheria*, 381  
*Krohnii*, *Cladonema*, 376  
*leuckarti*, *Protohydra*, 338  
*Lobocoryne*, 368  
*Margelopsidae*, 356  
*Margelopsis*, 356  
*mayeri*, *Cladonema*, 376  
*minor*, *Monocoryne*, 353  
*Monocoryne*, 351  
*myersi*, *Cladonema*, 380  
*Myriocnida*, 328  
*Myriothele*, 340  
*Myriotheleidae*, 340  
*nanna*, *Psammohydra*, 336  
*nematophora*, *Similomerona*, 325  
*novae-zelandiae*, *Cladonema*, 376  
*novaezelandiae*, *Cladonema*, 380  
*octonema*, *Eleutheria*, 381  
*pacificum*, *Cladonema*, 380  
*pelagica*, *Cladocoryne*, 370  
*Pelagohydra*, 356  
*Pelagohydridae*, 356  
*Pennaria*, 364  
*Pennariidae*, 363  
*pentanema*, *Eleutheria*, 381  
*perkinsii*, *Cladonema*, 376  
*phrygium*, *Candelabrum*, 346  
*Polycoryne*, 368  
*portmanni*, *Staurocladia*, 389  
*primarius*, *Acaulis*, 328  
*prolifera*, *Clavatella*, 381  
*Protohydra*, 338  
*Protohydridae*, 337  
*Psammocoryne*, 330  
*Psammohydra*, 336  
*purpurea*, *Spadix*, 341  
*radiatum*, *Cladonema*, 375  
*sargassensis*, *Cladocoryne*, 370  
*serpentarii*, *Candelabrum*, 341  
*Similomerona*, 325  
*simplex*, *Boreohydra*, 334  
*simplex*, *Cladocoryne*, 370  
*singularis*, *Tricyclusa*, 353  
*Spadix*, 341  
*Stauridia*, 375  
*stauridia*, *Coryne*, 376  
*Stauridium*, 375  
*stauridium*, *Syncoryne*, 376  
*Stauriidae*, 371  
*Staurocladia*, 372, 386  
*stylodendron*, *Dendronema*, 391  
*stylostoma*, *Margelopsis*, 353  
*Symplectanea*, 351  
*Symplectaneidae*, 340  
*tetranema*, *Eleutheria*, 381  
*Tiarella*, 353  
*Tricyclusa*, 353  
*Tricyclusidae*, 353  
*uchidai*, *Cladonema*, 380  
*ulvae*, *Herpusa*, 381  
*vallentini*, *Eleutheria*, 386  
*verrucosum*, *Candelabrum*, 349  
*Wandelia*, 386



## Identification biométrique des deux espèces sympatriques de souris *Mus musculus domesticus* et *Mus spretus* en Kabylie du Djurdjura (Algérie)

Nora KHAMMES<sup>1</sup>, Sovan LEK<sup>2</sup> & Stéphane AULAGNIER<sup>3</sup>

<sup>1</sup> Faculté des Sciences Biologiques et Agronomiques, Université Mouloud Mammeri, route d'Hassnaoua, 15000 Tizi-Ouzou, Algérie. E-mail: n\_khammes@hotmail.com

<sup>2</sup> Laboratoire Dynamique de la Biodiversité, Université Paul Sabatier, 118 route de Narbonne, F-31062 Toulouse cedex 4, France. E-mail: lek@cict.fr

<sup>3</sup> Comportement et Ecologie de la Faune Sauvage, B.P. 52627, F-31326 Castanet-Tolosan cedex, France. E-mail: aulagnie@toulouse.inra.fr

### **Biometrical identification of the sympatric mouse species *Mus musculus domesticus* and *Mus spretus* in Kabylie du Djurdjura (Algeria).**

This work aimed to validate biometric identification criteria (body and cranial measurements) for the two sympatric mouse species living in Algeria: the House mouse (*Mus musculus domesticus*) and the Algerian mouse (*M. spretus*). Trapped in three localities of Kabylie du Djurdjura, mice were first identified according to morphological criteria and second computing stepwise discriminant analyses and leave-one-out discriminant analyses on sets of the most relevant variables. Body measurements revealed more efficient than cranial measurements to discriminate the species. According to the original diagnosis of *M. spretus*, the Algerian mouse's tail was shorter than the House mouse's tail. The ratio 'tail length over head and body length' was highly discriminant (95% of correct classification); the score was still better (97%) when the diameter of the tail was included in the discriminant analysis. On the skull, the zygomatic ratio 'width of the dorsal ramus of the zygomatic arch over width of the zygomatic arch' was the only discriminant variable (90.4% of the correct classification). No identification was reliable with mandible measurements. Relevant discriminant values were then compared with values obtained from European samples.

**Keywords:** Algeria - biometrics - skull - discriminant analysis - *Mus spretus* - *Mus musculus domesticus*.

## INTRODUCTION

En 1846 déjà, Loche identifie deux espèces de souris en Algérie: *Mus musculus* et *Mus reboudi*, mais il s'est avéré par la suite que ces deux formes étaient conspécifiques. Puis, toujours en Algérie, Lataste (1883) décrit *Mus spretus* comme une nouvelle espèce, caractérisée par une oreille elliptique, une queue environ moitié plus

courte que le corps et un talon supplémentaire en avant de la première molaire. Mais plus tard (Lataste, 1887), il exprime des doutes à propos de cette différence spécifique, aussi par la suite *spretus* a souvent été considérée comme une sous-espèce d'une autre souris à queue courte *Mus spicilegus* Petenyi, 1882 (e.g. Miller, 1912; Cabrera, 1914, 1932) ou de *Mus musculus* Linnaeus, 1766 (e.g. Schwarz & Schwarz, 1943; Ellerman & Morrison-Scott, 1951).

Le statut spécifique de *Mus spretus* Lataste, 1883 a été rétabli lorsque vers la fin des années 70 deux espèces sympatriques de souris *Mus musculus domesticus* Ratty, 1772 et *Mus spretus* ont été différenciées génétiquement dans le sud de la France (Britton *et al.*, 1976, Britton & Thaller, 1978). Deux interrogations étroitement liées se sont immédiatement imposées: comment les identifier? où les trouver? Très rapidement, en étudiant la morphométrie externe et crânienne des animaux identifiés sur la base de leur polymorphisme enzymatique, des critères d'identification ont été proposés ou confirmés (Darviche, 1978; Marshall & Sage, 1981; Orsini, 1982; Darviche & Orsini, 1982). Parallèlement, l'examen des spécimens conservés en collection a permis de préciser l'aire de répartition de l'espèce en Afrique du Nord, dans la péninsule Ibérique et en France (Saint Girons & Thouy, 1978; Palomo *et al.*, 1983). Puis des travaux sur des populations naturelles et expérimentales ont permis d'appréhender les facteurs écologiques et comportementaux à l'origine de la sympatrie, voire de la syntopie de la Souris à queue courte avec le morphe (*brevirostris*) ou écotype sauvage de la Souris domestique, caractéristique de la région méditerranéenne (Orsini *et al.*, 1982, Cassaing, 1982, 1984; Cassaing & Croset, 1985).

De récentes synthèses ont fait le point sur l'identification des souris européennes (Gerasimov *et al.*, 1990; Macholán, 1996a, 1996b) ou françaises (Orsini *et al.*, 2001), mais aucune étude approfondie n'a été consacrée aux souris d'Afrique du Nord, alors que la plus grande diversité génétique locale des *Mus spretus* (Boursot *et al.*, 1985) peut laisser envisager une variabilité morphologique particulière.

C'est ce travail de calibration des critères d'identification morphométriques (biométrie externe et crânienne) des deux souris présentes en Algérie qui a été entrepris à partir d'un échantillon conséquent en provenance de trois stations de Kabylie du Djurdjura.

## MATÉRIEL ET MÉTHODES

### LOCALISATION DES STATIONS D'ÉTUDE

*Station 1:* village de Boukhalfa à 8 km de Tizi-Ouzou (36°42' N, 4°2' E; altitude: 500 m). Cette station est classée dans l'étage bioclimatique subhumide à hiver chaud. Située à proximité d'un verger, la végétation y est composée d'une strate arbustive haute à *Genista tricuspidata* et *Calycotome spinosa*, et une strate arbustive basse à *Rubus* sp. et *Cistus salvifolius*.

*Station 2:* village d'Attouche (commune de Makouda) à 25 km de Tizi-Ouzou (36°47' N, 4°3' E; altitude: 470 m). Cette station est classée dans l'étage bioclimatique subhumide à hiver doux. Délimitée par de grands rochers, cette station s'étend sur deux parcelles, l'une comprend essentiellement une strate herbacée et des affleurements rocheux, l'autre est occupée pour les grandes cultures céréalières, maraîchères et d'arbres fruitiers.

*Station 3:* village de Bou-Ilfane, au nord-est d'Azazga, à environ 45 km de Tizi-Ouzou (36°45' N, 4°27' E; altitude : 500 m). Cette station est classée dans l'étage bioclimatique subhumide à variante tempérée. C'est un maquis, formation dense issue de la dégradation de la forêt de Chêne liège *Quercus suber*, qui comprend principalement une strate arbustive constituée de *Myrtus communis*, *Genista tricuspidata*, *Cistus monspeliensis*, *Erica arborea* et *Calycotome spinosa*.

#### ANIMAUX

Le nombre total d'individus capturés au moyen de surfaces engluées (Tripathi *et al.*, 1994) est de 138 souris des deux espèces pour 1200 nuits-pièges (longueur totale des lignes de pièges: 6000 mètres). En retirant les juvéniles (usure dentaire nulle, Keller, 1974; Palomo *et al.*, 1981) dont la croissance n'est pas terminée, le nombre d'animaux étudiés est de 101, soit 33 + 20 + 2 *Mus musculus domesticus* et 28 + 12 + 6 *Mus spretus* (stations 1 + 2 + 3). Les deux espèces ont été identifiées en fonction du nombre de plis palatins (avant la préparation ostéologique du crâne): *Mus spretus* possède six rangées de plis palatins alors que *Mus musculus domesticus* en possède sept (Darviche, 1978; Orsini, 1982).

#### MESURES

Les animaux ont été mesurés en utilisant un pied à coulisse au 1/10 mm pour les mensurations corporelles, au 1/100 mm pour les mensurations crâniennes et mandibulaires, et une loupe binoculaire munie d'un micromètre au 1/100 mm pour les mensurations dentaires.

Les mensurations corporelles ont été prises sur l'animal maintenu à plat sur le ventre après sa capture: longueur de la tête et du corps (T+C), longueur de la queue (Q), longueur du pied postérieur (Pp), longueur de l'oreille (Or) et diamètre de la queue (DQ); le rapport  $Q / T+C$  a été calculé.

Vingt-six variables crâniennes et dentaires inspirées des travaux de Sans-Coma *et al.* (1979), Thorpe *et al.* (1982), Darviche & Orsini (1982), Davis (1983), Palomo *et al.* (1983) et Lyalyukhina *et al.* (1991) ont été relevées: longueur du crâne (Lcr), longueur et largeur du nasal (Ln, ln), largeur bizygomatique (lbz), largeur interorbitaire (io), largeur bisquamosale (lsq), largeur du foramen occipital (focc), longueur et largeur de la bulle tympanique (Lbul, lbul), hauteur postérieure du crâne (hcr), longueur du foramen palatin (fopal), largeur du palais (lpal), longueur incisivo-palatine (de l'avant des incisives à l'arrière du palais) (Lipa), largeur du ramus dorsal de l'arcade zygomatique (lraz), largeur de l'arcade zygomatique (laz), coefficient zygomatique ( $coz = lraz/laz$ ), longueur de l'orbite (Lorb), largeur du crâne (lcr), longueur du diastème supérieur (diasup), longueur de la rangée molaire supérieure (rms), longueur de la rangée molaire inférieure (rmi), hauteur de la mandibule (hm), longueur du diastème inférieur (diainf), longueur de la mandibule (Md), longueur et largeur de la première molaire inférieure (Lm1, lm1).

#### ANALYSE STATISTIQUE

Outre des statistiques descriptives et tests de Student, l'identification des deux espèces a été réalisée au moyen d'une analyse discriminante pas à pas qui sélectionne successivement la (puis les) variable(s) la (les) plus discriminante(s), complétée par une analyse discriminante avec validation croisée qui détermine l'affectation de



chaque individu à partir de l'apprentissage réalisé sur tous les autres. Les calculs ont été effectués avec le logiciel SPSS Professional Statistics 6.1 (Norusis, 1994).

## RÉSULTATS

### BIOMÉTRIE CORPORELLE

Toutes les variables corporelles, à l'exception de la longueur du pied postérieur, différencient très significativement les deux espèces (Tableau 1), tout en restant faiblement corrélées. La Souris d'Afrique du Nord a une queue plus courte que la longueur tête plus corps contrairement à la Souris domestique qui a une queue plus longue que la longueur tête plus corps. Le rapport Q/T+C, qui permet classiquement de caractériser chacune des deux espèces varie de 0,48 à 0,99 chez *Mus spretus* et de 0,93 à 1,31 chez *Mus musculus domesticus*. De fait, les mesures de la queue permettent objectivement de déterminer la quasi totalité des individus. Toutefois la première analyse

TABLEAU 1. Mensurations des deux espèces de souris, *Mus musculus domesticus* et *Mus spretus* en Kabylie du Djurdjura (Algérie) (n: effectif de l'échantillon; min: minimum; moy: moyenne; max: maximum; Et: écart-type; t: test de Student; ddl: degrés de liberté; s: seuil de signification du test de Student).

	<i>Mus musculus domesticus</i>					<i>Mus spretus</i>							
	N	min	moy	Max	Et	n	min	moy	max	Et	t	ddl	s
T+C	55	50,0	65,81	86,0	10,93	46	60,0	76,77	98,0	11,43	612,54	99	0,000
Q	55	52,5	71,20	88,5	11,91	46	44,6	57,83	70,5	7,46	584,60	99	0,000
Pp	55	15,0	18,55	20,1	1,08	46	14,8	16,38	19,6	1,56	2,97	99	0,098
Or	55	11,9	13,53	15,0	0,77	46	10,0	12,76	15,5	1,53	6,06	99	0,000
DQ	55	1,8	2,74	3,7	0,40	46	1,5	1,98	2,5	0,24	8,42	99	0,000
Q / T+C	55	0,9	1,08	1,3	0,08	46	0,4	0,77	0,9	0,12	7,11	99	0,000
Lcr	38	15,61	19,57	21,90	1,74	38	17,38	20,38	22,90	1,22	9,36	74	0,000
Ln	50	5,62	7,21	9,00	0,74	45	5,85	7,67	9,72	0,91	2,93	93	0,000
ln	50	1,72	2,29	2,88	0,27	45	1,54	2,57	3,60	0,48	1,51	93	0,074
lbz	38	7,55	9,39	10,10	0,53	41	8,49	9,47	10,10	0,40	1,15	77	0,523
io	44	2,99	3,76	4,89	0,33	46	2,99	3,79	4,96	0,42	1,73	88	0,523
lsq	38	7,42	8,59	9,43	0,53	38	8,29	9,11	9,83	0,44	1,22	74	0,360
focc	40	3,63	4,54	5,71	0,60	38	3,48	4,47	5,58	0,63	1,49	76	0,063
Lbul	38	2,76	3,98	5,32	0,53	29	2,99	3,98	5,17	0,60	1,25	65	0,304
lbul	38	2,14	3,07	4,52	0,50	29	2,30	2,97	4,15	0,52	1,03	65	0,879
hcr	38	6,33	7,46	8,34	0,48	35	6,57	7,39	7,97	0,39	1,30	71	0,251
fopal	47	3,10	3,96	6,16	0,61	45	3,12	4,78	6,5	0,84	2,79	90	0,000
lpal	46	2,00	2,70	3,79	0,32	46	2,21	2,80	3,96	0,34	2,28	90	0,000
Lipa	46	6,81	8,88	12,10	0,97	45	8,01	9,81	11,1	0,76	3,90	89	0,000
lraz	47	0,22	0,41	0,84	0,11	46	0,27	0,57	0,81	0,12	11,98	91	0,000
laz	47	0,48	0,84	1,80	0,24	46	0,36	0,76	1,06	0,14	6,15	91	0,000
coz	47	0,33	0,49	0,64	0,07	46	0,52	0,75	1,06	0,13	8,65	91	0,000
Lorb	39	5,05	6,27	7,26	0,59	42	4,64	6,75	7,66	0,61	1,66	79	0,215
lcr	46	4,55	6,59	9,37	0,96	46	3,96	6,83	9,57	1,34	5,46	90	0,000
diasup	47	3,55	4,87	6,03	0,60	45	4,32	5,11	6,26	0,39	1,09	90	0,667
rms	49	2,69	3,14	3,90	0,20	46	2,99	3,18	3,34	0,08	2,61	93	0,072
rmi	55	2,72	2,90	3,03	0,09	46	2,05	2,90	3,97	0,23	3,58	99	0,140
hm	53	3,43	4,72	5,96	0,66	41	3,12	4,65	5,80	0,69	1,83	92	0,162
diainf	55	2,45	3,07	5,46	0,43	46	2,25	3,15	5,17	0,49	1,19	99	0,374
Md	53	8,05	10,18	12,0	1,01	46	8,85	10,68	12,2	0,77	3,53	97	0,032
Lml	55	1,12	1,31	1,48	0,08	46	0,88	1,36	1,68	0,17	13,40	99	0,000
lm1	55	0,88	1,06	1,20	0,06	46	0,96	1,04	1,12	0,04	7,74	99	0,841

discriminante retient trois variables corporelles dans l'ordre suivant: diamètre de la queue, rapport Q/T+C et longueur de l'oreille avec un résultat remarquable tant en apprentissage qu'en validation croisée (Tableau 2). Avec le seul rapport Q/T+C, la discrimination des deux espèces est très bonne, elle devient excellente en rajoutant le diamètre de la queue (seul un individu est mal classé en apprentissage, contre trois en validation croisée).

#### BIOMÉTRIE CRÂNIENNE

La majorité des variables crâniennes ne sont pas significativement différentes d'une espèce à l'autre. Sont significativement différentes: la longueur du crâne, la longueur du nasal, la longueur du foramen palatin, la largeur du palais, la longueur incisivo-palatine, la largeur du ramus dorsal de l'arcade zygomatique, la largeur de l'arcade zygomatique (et le coefficient zygomatique), la largeur du crâne, la longueur de la mandibule et la longueur de la première molaire inférieure.

Les variables crâniennes apparaissent relativement corrélées entre elles, à l'exception des rangées molaires supérieure (rms) et inférieure (rmi), des largeurs interorbitaire (io) et bizygomatique (bz), de la longueur de la première molaire inférieure (Lm1), seulement corrélée à la largeur de cette même dent (bm1,  $r=0,59$ ). Les variables les plus corrélées sont la longueur du crâne (Lcr) et la longueur incisivo-palatine (Lipa,  $r=0,66$ ), et surtout la largeur du ramus dorsal de l'arcade zygomatique (lraz) et le coefficient zygomatique (coz,  $r=0,78$ ).

L'analyse discriminante pas-à-pas (90,4% de bon classement en apprentissage et en validation croisée) retient une seule variable: le coefficient zygomatique (coz). L'exclusion du coefficient zygomatique de l'analyse conduit à un modèle moins performant qui repose encore sur les mesures de l'arcade zygomatique avec pour complément la largeur bizygomatique et la longueur incisivo-palatine (Tableau 2). Fort heureusement l'arcade zygomatique est relativement robuste et pourra être mesurée sur les crânes issus de pelotes de réjection de rapaces, notamment de Chouette effraie (*Tyto alba*), de Hibou moyen-duc (*Asio otus*) ou de Chouette hulotte (*Strix aluco*).

Les deux analyses discriminantes effectuées sur les mensurations de la mandibule ne peuvent être retenues, les pourcentages de classement, tant en apprentissage qu'en validation croisée, étant trop faibles (Tableau 2). Il apparaît donc impossible d'identifier avec une incertitude raisonnable des mandibules isolées édentées, telles qu'on les trouve souvent dans les pelotes de réjection de rapaces ou bien dans les fèces de carnivores.

#### DISCUSSION

Il ressort de ce travail que la biométrie corporelle apparaît plus performante que la biométrie crânienne pour discriminer les deux espèces de souris présentes en Kabylie du Djurdjura. Conformément à la description originale de *Mus spretus*, cette souris possède une queue plus courte que *Mus musculus domesticus* ( $57,83 \pm 7,46$  mm vs  $71,20 \pm 11,91$  mm), le rapport de la longueur de la queue sur la longueur tête plus corps permet de séparer nettement les deux espèces. Compris entre 0,77 et 0,99 chez la souris à queue courte, il est de 0,93 à 1,31 chez la souris domestique. De plus la queue de *Mus spretus* est toujours plus fine que celle de *M. m. domesticus*. La combi-

TABLEAU 2. Identification des deux espèces de souris en Kabylie du Djurdjura: résultats des analyses discriminantes sur les variables de morphologie externe et crânienne (pourcentages de classement en apprentissage (% Appr.) et en validation croisée (% Valid.), et principales fonctions discriminantes, A: *Mus musculus domesticus*, B: *Mus spretus*; si A est supérieur à B l'animal est *Mus musculus domesticus*, si B est supérieur à A l'animal est *Mus spretus*).

Variabes	% Appr.	% Valid.	Fonctions discriminantes
<b>Biométrie corporelle</b>			
DQ, Q / T+C, Or	99,0	98,0	A = 16,220 DQ + 112,007 Q / T + C + 11,864 Or - 164,693 B = 11,641 DQ + 83,084 Q / T + C + 10,667 Or - 111,387
Q / T+C	95,0	95,0	A = 78,781 Q/T+C - 43,686 B = 54,119 Q/T+C - 20,982
Q / T+C, DQ	99,0	97,0	A = 15,702 DQ + 83,633 Q / T+C - 68,249 B = 11,175 DQ + 57,572 Q / T+C - 33,423
<b>Biométrie crânienne</b>			
COZ	90,4	90,4	A = 48,247 COZ - 12,559 B = 72,904 COZ - 27,787
lbz, lraz, laz, Lipa	92,2	88,3	
Lm1, lm1	71,3	70,3	
Md, hm	62,0	60,9	

DQ: diamètre de la queue; Q / T+C: rapport de la longueur de la queue (Q) sur la longueur de la tête et du corps (T+C); Or: longueur de l'oreille; COZ (coefficient zygomatique): rapport de la largeur du ramus dorsal de l'arcade zygomatique (lraz) sur la largeur de l'arcade zygomatique (laz); lbz: largeur bizygomatique; Lipa: longueur incisivo-palatine (de l'avant des incisives à l'arrière du palais); Lm1-lm1: longueur et largeur de la première molaire inférieure; Md: longueur de la mandibule; hm: hauteur de la mandibule.

naison des deux variables fournit les meilleures fonctions dicriminantes. Ces résultats sont conformes aux données publiées sur les spécimens d'Europe (Orsini *et al.*, 1982; Darviche & Orsini 1982; Palomo *et al.*, 1981), avec toutefois un intervalle différent pour le rapport de la longueur de la queue sur la longueur tête plus corps (0,6-0,8 pour *Mus spretus*, 0,75-1,05 pour *Mus musculus domesticus*). Cette différence est liée à la longueur tête plus corps, significativement plus faible chez les souris domestiques d'Algérie ( $65,95 \pm 11,54$  mm contre  $76,52 \pm 11,72$  mm pour les souris à queue courte), alors qu'en Europe Orsini *et al.* (2001) rapportent des longueurs très proches ( $75,44 \pm 1,83$  mm et  $75,86 \pm 2,00$  mm respectivement). Orsini *et al.* (2001) évoquent par contre la longueur plus réduite des membres de *Mus spretus*, ce qui renforce l'impression de petite taille chez cette espèce. En Algérie la différence n'est pas significative.

Sur le crâne, le coefficient zygomatique, rapport de la largeur du ramus dorsal de l'arcade zygomatique sur la largeur de l'arcade zygomatique, est la meilleure variable pour la discrimination des deux espèces sympatrique (0,33 à 0,64 chez *Mus musculus domesticus*, 0,60 à 1,06 chez *Mus spretus*). Pour les populations européennes il était déjà considéré comme discriminant par Darviche & Orsini (1982) et Orsini *et al.* (1983), avec cependant une valeur seuil de 0,70 ( $0,79 \pm 0,14$  chez *Mus spretus* et  $0,50 \pm 0,08$  chez *Mus musculus domesticus* (Orsini *et al.*, 2001). Macholán (1996b) a



en outre relevé une hauteur du crâne plus élevée chez *Mus musculus domesticus*, alors que cette mensuration n'est pas significativement différente chez les souris algériennes. Enfin, la longueur et la largeur de la première molaire inférieure, qui permettent de séparer les deux espèces de souris selon ce même auteur, ne fournissent pas une discrimination satisfaisante pour les spécimens algériens, en dépit de la longueur significativement supérieure observée chez *Mus spretus*. Il reste que pour les mandibules, le dessin de la surface d'usure de cette dent constitue un critère d'identification supplémentaire, quoique parfois délicat (Orsini, 1979).

## CONCLUSION

Hormis quelques légères différences pour certaines variables (longueur tête plus corps notamment) qu'il faudra confirmer sur des échantillons en provenance d'autres régions, les deux espèces de souris de Kabylie du Djurdjura peuvent être distinguées sur la base des critères reconnus en Europe : rapport de la longueur de la queue et de la longueur tête plus corps en association avec le diamètre de la queue pour la biométrie corporelle et le coefficient zygomatique pour la biométrie crânienne. La fiabilité des identifications permet d'envisager des études sur l'écologie et la biologie des populations des deux espèces, qui semblent particulièrement inféodées aux activités anthropiques en Afrique du Nord (Aulagnier & Thévenot, 1986; Khidas, 1993; Khidas *et al.*, 1999). L'identification des proies des rapaces s'en trouve également facilitée, les différents caractères morphologiques proposés (synthèse dans Macholán, 1996b et Orsini *et al.*, 2001) n'étant pas toujours accessibles.

## REMERCIEMENTS

Ce travail a été réalisé dans le cadre de l'accord – programme franco-algérien 99MDU423.

## BIBLIOGRAPHIE

- AULAGNIER, S. & THÉVENOT, M. 1986. Catalogue des Mammifères sauvages du Maroc. *Travaux de l'Institut Scientifique, Rabat* 41: 1-163.
- BOURSOT, P., JACQUART, T., BONHOMME, F., BRITTON-DAVIDIAN, J. & THALER, L. 1985. Différenciation géographique du génome mitochondrial chez *Mus spretus* Lataste. *Comptes Rendus de l'Académie des Sciences de Paris, Série III*, 301: 161-166.
- BRITTON, J., PASTEUR, N. & THALER, L. 1976. Les souris du midi de la France: caractérisation génétique de deux groupes de populations sympatriques. *Comptes Rendus de l'Académie des Sciences de Paris, Série III*, 283: 515-518.
- BRITTON, J. & THALER, L. 1978. Evidence for the presence of two sympatric species of mice (genus *Mus* L.) in southern France based on biochemical genetics. *Biochemical Genetics* 16: 214-225.
- CABRERA, A. 1914. Fauna ibérica. Mamíferos. *Museo nacional de Ciencias naturales, Madrid*, 441 pp.
- CABRERA, A. 1932. Los Mamíferos de Marruecos. *Trabajos del Museo nacional de Ciencias naturales, Seria Zoologia* 57: 1-361.
- CASSAING, J. 1982. Les populations sauvages de souris du Midi de la France (*Mus domesticus* et *Mus spretus*) : Approche étho-écologique et conséquences évolutives. Thèse 3<sup>e</sup> Cycle (*Evolution et Biosystématique*), Université des Sciences et Techniques du Languedoc, Montpellier, 158 pp.

- CASSAING, J. 1984. Interactions intra et inter spécifiques chez les souris sauvages du midi de la France, *Mus musculus domesticus* et *Mus spretus*: conséquences sur la compétition entre les deux espèces. *Biology of Behaviour* 9: 281-293.
- CASSAING, J. & CROSET, H. 1985. Organisation spatiale, compétition et dynamique des populations sauvages de souris (*Mus spretus* Lataste et *Mus musculus domesticus* Ratty) du Midi de la France. *Zeitschrift für Säugetierkunde* 50: 271-284.
- DAVIS, S.J.M. 1983. Morphometric variation of populations of house mice *Mus domesticus* in Britain and Faroe. *Journal of Zoology, London* 199: 521-534.
- DARVICHE, D. 1978. Approche morphologique et biométrique de la biosystématique à la lumière de la génétique biochimique des populations. Application aux genres *Mus* et *Apodemus* (Mammalia, Rodentia). Thèse 3<sup>e</sup> Cycle (Evolution et Biosystématique), Université des Sciences et Techniques du Languedoc, Montpellier, 191 pp.
- DARVICHE, D. & ORSINI, P. 1982. Critères de différenciation morphologique et biométrique de deux espèces de souris sympatriques: *Mus spretus* et *Mus musculus domesticus*. *Mammalia* 46: 205-217.
- ELLERMAN, J.R. & MORRISON-SCOTT, T.C.S. 1951. Checklist of Palearctic and Indian Mammals 1758 to 1946. *British Museum (Natural History), London*, 810 pp.
- GERASIMOV, S., NIKOLOV, H., MIHAILOVA, V., AUFRAY, J.C. & BONHOMME, F. 1990. Morphometric stepwise discriminant analysis of the five genetically determined European taxa of the genus *Mus*. *Biological Journal of the Linnean Society* 41: 47-64.
- KELLER, A. 1974. Détermination de l'âge de *Mus musculus* Linné par l'usure de la dentition. *Revue suisse de Zoologie* 81: 839-844.
- KHIDAS, K. 1993. Distribution des rongeurs en Kabylie du Djurdjura (Algérie). *Mammalia* 57: 207-212.
- KHIDAS, K., KHAMMES, N. & KHELLOUFI, S. 1999. Répartition spatiale et sélection de l'habitat chez le mulot sylvestre (*Apodemus sylvaticus* Linnaeus, 1758) et la souris sauvage (*Mus spretus* Lataste, 1883) en Kabylie du Djurdjura (Algérie). *Sciences & Technologie* 12: 59-64.
- LATASTE, F. 1883. Note sur les souris d'Algérie et description d'une espèce nouvelle (*Mus spretus*). *Actes de la Société Linnéenne de Bordeaux* 37: 13-35.
- LATASTE, F. 1887. Catalogue critique des mammifères apélagiques de Tunisie. In: Exploration scientifique de la Tunisie. *Imprimerie nationale, Paris*, XV + 42 pp.
- LOCHE, V. 1846. Sciences physiques, Zoologie. Histoire naturelle des mammifères. In: Exploration scientifique de l'Algérie pendant les années 1840, 1841, 1842. *Imprimerie royale, Paris*, 123 pp.
- LYALYUKHINA, S., KOTENKOVA, E., WALKOWA, W. & ADAMCZYK, K. 1991. Comparison of cranio-logical parameters in *Mus musculus musculus* Linnaeus, 1758 and *Mus hortulanus* Nordmann, 1840. *Acta Theriologica* 36: 95-107.
- MACHOLÁN, M. 1996a. Morphometric analysis of European house mice. *Acta Theriologica* 41: 255-275.
- MACHOLÁN, M. 1996b. Key to European house mice (*Mus*). *Folia Zoologica*, 45: 209-217.
- MARSHALL, J. T. & SAGE, R.D. 1981. Taxonomy of the house mouse. *Symposium of the Zoological Society of London* 47: 15-25.
- MILLER, G.S. 1912. Catalogue of the mammals of the Western Europe (Europe exclusive of Russia) in the collection of the British Museum. *British Museum (Natural History), London*, 1019 pp.
- NORUSIS, M.J. 1994. SPSS: SPSS Professional Statistics 6. *S.P.S.S. Inc., Chicago*, 385 pp.
- ORSINI, P. 1979. Notes sur les souris de Provence. *Annales de la Société de Sciences naturelles et d'Archéologie de Toulon et du Var* 31: 168-173.
- ORSINI, P. 1982. Facteurs régissant la répartition des souris en Europe: intérêt du modèle souris pour une approche des processus évolutifs. Thèse 3<sup>e</sup> Cycle (Evolution et Biosystématique), Université des Sciences et Techniques du Languedoc, Montpellier, 134 pp.

- ORSINI, P., CASSAING, J., DUPLANTIER, J.M. & CROSET, H. 1982. Premières données sur l'écologie des populations naturelles de souris, *Mus spretus* Lataste et *Mus musculus domesticus* Rutty dans le Midi de la France. *Terre et Vie* 36: 321-335.
- ORSINI, P., FAUGIER, C. & BUTET, A. 2001. Identification des Insectivores et Rongeurs de France: les espèces jumelles de souris, *Mus musculus domesticus* et *Mus spretus*. *Arvicola* 13: 9-11.
- PALOMO, L.J., ESPAÑA, M., LOPEZ-FUSTER, M.-J., GOZALBEZ, J. & SANS-COMA, V. 1981. Sobre la variabilidad fenética y morfométrica de *Mus spretus* Lataste, 1883 en la Peninsula Ibérica. *Miscellanea Zoologica* 7: 171-192.
- SANS-COMA, V., LOPEZ-FUSTER, M. J. & GOSALBEZ, J. 1979. Über die Hausmans, *Mus musculus* Linné; 1758, auf der Insel Meda Crossa Katalonien, Spanien. *Säugetierkundliche Mitteilungen*, 27: 107-113.
- SAINT GIRONS, M.C. & THOUY, P. 1978. Fluctuations dans les populations de souris *Mus spretus* Lataste 1883, en région méditerranéenne. *Bulletin d'Ecologie* 9: 211-218.
- SCHWARZ, E. & SCHWARZ, H.K. 1943. The wild and commensal stocks of the house mouse, *Mus musculus* Linnaeus. *Journal of Mammalogy* 24: 59-72.
- THORPE, R.S., CORTI, M. & CAPANNA, E. 1982. Morphometric divergence of Robertsonian populations/species of *Mus*: A multivariate analysis of size and shape. *Experientia* 38: 920-923.
- TRIPATHI, R.S., MATHUR, M., JAIN, A.P. & PATEL, N. 1994. Relative efficacy of glue and other traps for commensal rodent management. *Annals of arid Zone* 33: 143-145.





## A review of *Capoeta tinca*, with descriptions of two new species from Turkey (Teleostei: Cyprinidae)

Davut TURAN<sup>1</sup>, Maurice KOTTELAT<sup>2</sup>, F. Güler EKMEKÇİ<sup>3</sup> & H. Oguz IMAMOGLU<sup>1</sup>

<sup>1</sup> Karadeniz Technical University, Faculty of Fisheries and Aquatic Sciences, 53100 Rize, Turkey. E-mail: davutturan61@hotmail.com

<sup>2</sup> Corresponding author, Route de la Baroche 12, CH-2952 Cornol, Switzerland (permanent address) and Raffles Museum of Biodiversity Research, National University of Singapore, Kent Ridge, Singapore 119260. E-mail: mkottelat@planet.ch

<sup>3</sup> Department of Biology, Faculty of Sciences, Hacettepe University, Beytepe Campus, 06532 Ankara, Turkey. E-mail: gulere@hacettepe.edu.tr

**A review of *Capoeta tinca*, with descriptions of two new species from Turkey (Teleostei: Cyprinidae).** - Fishes previously referred to *Capoeta tinca* in Turkey and Georgia belong to three species: *C. tinca* in rivers draining to the Marmara Sea, *C. baliki*, new species, in rivers draining to the southwestern Black Sea, and *C. banarescui*, new species, in the Çoruh River drainage. *Capoeta banarescui* is distinguished by missing sexual dimorphism in the mouth shape (present in the two other species) and fewer and larger scales. *Capoeta baliki* is distinguished by its more slender body and caudal peduncle, and blunter head.

**Keywords:** New species - Cyprinidae - *Capoeta* - Çoruh River - Sakarya River - Kızılırmak River - Anatolia.

## INTRODUCTION

Heckel (1843) described *Scaphiodon tinca* from "Brussa in Natolien", the present city of Bursa, in the Nilüfer drainage, a stream flowing to the Sea of Marmara in Turkey. Günther (1868), Steindachner (1897), Berg (1949), and Kosswig & Battalgil (1943) reported this species as *Varicorhinus tinca* from Bursa, Ankara, Eskşehir, Sakarya and Trabzon. Karaman (1969) revised the genus *Varicorhinus* and placed *V. tinca* in the genus *Capoeta*. Since, several authors have reported *C. tinca* from central and northern Anatolia (e.g., Kuru, 1975; Balık, 1979; Erk'akan, 1981; Kutrup, 1994). Although these authors examined different populations, all recorded somewhat similar lateral line scale and gill raker counts.

Banarescu & Herzig-Straschil (1999) redescribed *C. tinca* and mentioned considerable differences between specimens from Çoruh drainage (northeastern Anatolia) and those from western and central Anatolia. We have compared the different populations which have been referred to *C. tinca* and conclude that they are in fact three species. The Çoruh and Sakarya populations are described as two new species, *C. banarescui* and *C. baliki*, respectively.

## MATERIAL AND METHODS

Fish were caught with pulsed DC electrofishing equipment. Material is deposited in: ESFM, Museum of the Faculty of Fisheries, Ege University, Izmir; FFR, Zoology Museum of the Faculty of Fisheries, Karadeniz Technical University, Rize; and CMK, the collection of the second author. Additional material is preserved in the collection of the third author. Measurements were taken with digital calipers (0.1 mm accuracy). Counts and measurements follow Hubbs & Lagler (1947) except as follows. Head width<sub>1</sub>: distance between anterior margin of eye; head width<sub>2</sub>: distance between posterior margin of eyes; snout width: measured at level of nostril. Lateral line scale count includes scales on the base of the caudal fin. Vertebrae count includes the four Weberian vertebrae and the hypural complex. The last two branched anal and dorsal-fin rays articulating on the same pterygiophore are counted as one.

### *Capoeta tinca* (Heckel, 1843)

Fig. 1

*Capoeta tinca* Heckel, 1843: 1021 (type locality: "Brussa in Natolien"; lectotype: Naturhistorisches Museum Wien 55931:1, designated by Banareescu & Herzig-Straschil, in Banareescu, 1999: 413).

**MATERIAL EXAMINED:** FFR 717, 2, 145-157 mm SL; Turkey: Bursa: Nilüfer River, 40°15'N 28°55'E; D. Turan & S. G. Kirankaya, 15 September 2004. - FFR 718, 23, 116-201 mm; CMK 18538, 10, 113-179 mm SL; Turkey: Balıkesir: Koca River, Manyas, 40°05'N 28°02'E; D. Turan & S. G. Kirankaya, 14 September 2004.

**DIAGNOSIS:** *Capoeta tinca* is distinguished from the other species of the genus by the combination of the following characters: two pairs of barbels; snout rounded; 69-80 lateral line scales; 14-17 scales rows between lateral line and dorsal-fin origin, 12-14 between lateral line and anal-fin origin; 19-23 gill rakers on the first gill arch; lower jaw slightly arched in males, straight in females; head length 23.3-26.7% SL; depth of caudal peduncle 10.8-13.4% SL; head width at posterior margin of eye 49.3-56.5% HL; snout depth at nostril 30.0-41.1% HL; length of anterior barbel 8.1-14.1% HL and posterior barbel 11.5-19.3% HL.

**DESCRIPTION:** See Figure 1 for general appearance and Tables 1-2 for morphometric and meristic data. Dorsal head profile convex. Snout rounded, blunt, triangular in ventral view, depth slightly smaller than width at nostrils. Mouth wide, shape sexually dimorphic, arched in male, straight in female (Fig. 2). Rostral fold well developed, partly hiding upper lip. Upper and lower lips adnate to jaws, lower jaw covered with horny sheath. No tubercles on head. Anterior barbel not reaching corner of mouth. Posterior barbel reaching about middle of eye. Predorsal profile of body convex. Body high and weakly compressed.

Dorsal fin with 3 or 4 simple and 8 branched rays, outer margin slightly emarginate, origin slightly in front of vertical through pelvic-fin origin, last simple ray moderately ossified, proximal two thirds rigid, and with 24-28 serrae on posterior margin (Fig. 3a). Pectoral fin with 18-20 branched rays. Pelvic fin with 1 simple and 8-9 branched rays. Anal fin with 3 simple and 5 branched rays, outer margin convex. Caudal fin long and deeply forked. Gill rakers, 6-7 + 1 + 12-15 = 19-23 on outer side of first arch, number increasing with size (19, in 6 specimens about 125 mm SL; 20, in 8 specimens about 136 mm SL; 21, in 4 specimens about 145 mm SL; 22, in 5 spe-





FIG. 1

*Capoeta tinca*, FFR 718, 129 mm SL; Turkey: Koca River.



FIG. 2

*Capoeta tinca*, FFR 718, female, 129 mm SL (left) and male, 136 mm SL (right).

cimens about 160 mm SL; 23, in 2 specimens about 200 mm SL). 69-80 lateral line scales, 14-17 between dorsal-fin origin and lateral line and 9-11 between anal-fin origin and lateral line. 44-46 (modally 45) total vertebrae.

**SEXUAL DIMORPHISM:** Males collected in September have no tubercles on side and tip of snout, and on cheeks. Mouth slightly arched in male, straight in female.

**COLORATION:** Live and formalin preserved specimens dark brown on back and flanks, yellowish white on belly. Each scale margined by a band of black pigments, forming a regular reticulated pattern. Dorsal and caudal fins grey; pectoral, pelvic and anal fins whitish.

TABLE 1. Morphometry of the species of the *Capoeta tinca* group and *C. antalyensis*.

Basin Drainage	<i>C. tinca</i>		<i>C. baliki</i>		<i>C. banarescui</i>		<i>C. antalyensis</i>	
	Marmara Sea Nilüfer R. n=2	Kocaa R. n=24	Southern Black Sea Sakarya R. n=25	Kızılırmak R. n=10	Northeastern Black Sea Çoruh R. n=26	Mediterranean Gökdere R. n=10		
In percents of standard length								
Head length	24.6-25.1 (24.8)	23.3-26.7 (24.9)	21.9-24.8 (23.5)	22.5-24.7 (23.6)	22.2-25.8 (24.4)	23.3-26.2 (24.9)		
Body depth of dorsal-fin origin	26.0-26.1 (26.1)	24.4-28.0 (26.0)	21.2-24.9 (23.2)	19.8-23.5 (22.0)	21.4-25.1 (23.0)	23.1-25.5 (24.3)		
Predorsal length	50.1-51.8 (51.3)	48.0-53.4 (51.0)	48.6-55.5 (51.3)	46.5-53.4 (50.1)	48.7-54.5 (50.6)	50.4-54.2 (52.2)		
Postdorsal length	37.1-38.1 (37.6)	34.8-39.3 (37.3)	34.4-38.8 (36.6)	33.3-41.4 (37.4)	34.9-40.1 (37.2)	36.2-38.3 (37.1)		
Prepelvic length	53.5-54.3 (53.9)	52.4-57.8 (54.5)	51.8-56.7 (54.1)	51.8-55.3 (53.1)	50.5-57.3 (54.7)	54.3-56.7 (55.7)		
Precanal length	76.1-76.7 (76.4)	74.9-79.8 (77.0)	74.7-79.3 (77.0)	73.7-82.5 (76.4)	73.3-79.9 (76.3)	76.9-78.8 (77.7)		
Pectoral-fin origin to anal fin	54.8-55.2 (55.0)	52.6-57.6 (55.1)	52.3-58.4 (55.3)	45.5-58.4 (53.9)	50.3-58.2 (54.7)	54.8-58.4 (56.1)		
Pectoral-fin origin to pelvic fin	29.9-31.6 (30.7)	30.1-34.9 (32.0)	28.9-34.0 (32.0)	29.2-34.3 (31.3)	29.1-35.3 (33.0)	31.7-34.2 (33.3)		
Pelvic-fin origin to anal fin	22.0-25.7 (23.8)	20.9-26.2 (23.5)	22.1-24.4 (23.3)	20.5-25.4 (22.9)	18.5-23.6 (21.5)	21.3-24.3 (23.0)		
Dorsal-fin height	18.7-19.3 (19.0)	17.4-21.9 (19.2)	15.6-21.1 (18.3)	16.9-20.8 (17.9)	15.9-20.7 (18.6)	16.7-20.1 (18.9)		
Anal-fin length	16.2-20.9 (18.6)	17.0-21.7 (18.8)	15.1-21.3 (17.0)	15.2-20.8 (17.9)	15.9-21.8 (18.7)	14.7-18.1 (16.5)		
Pectoral-fin length	18.4-18.7 (18.6)	17.3-21.3 (18.9)	16.5-19.5 (18.3)	17.2-19.7 (18.5)	16.2-21.6 (19.4)	17.5-19.4 (18.7)		
Pelvic-fin length	16.4-16.6 (16.5)	15.2-17.7 (16.5)	14.4-16.8 (15.8)	14.7-17.4 (15.8)	14.0-17.0 (15.9)	14.4-17.1 (16.1)		
Upper caudal-fin lobe	24.3-24.3 (24.3)	22.8-26.6 (24.7)	19.3-24.6 (22.3)	22.8-26.1 (24.9)	20.3-25.5 (22.9)	21.1-24.2 (22.8)		
Length of middle caudal-fin rays	13.1-14.8 (13.9)	13.1-15.7 (14.2)	11.6-14.7 (13.4)	13.3-15.7 (14.2)	10.6-15.1 (13.3)	12.3-14.6 (13.4)		
Length of caudal peduncle	16.7-17.3 (16.9)	15.4-18.5 (16.8)	16.0-20.2 (17.6)	16.3-18.2 (17.4)	15.5-19.9 (17.4)	16.9-19.8 (18.4)		
Depth of caudal peduncle	11.2-11.4 (11.9)	10.8-13.4 (11.7)	9.7-12.3 (10.9)	9.5-11.1 (10.3)	9.8-11.7 (10.7)	11.2-12.4 (11.6)		
In percents of head length								
Snout length	36.7-36.7 (36.7)	33.1-40.4 (37.3)	33.7-40.6 (37.3)	36.2-43.4 (39.6)	35.4-41.2 (38.3)	35.7-41.7 (38.6)		
Eye diameter	16.3-16.7 (14.5)	14.2-18.6 (16.3)	13.1-18.8 (15.9)	14.6-19.3 (16.6)	13.2-18.9 (15.1)	16.0-19.0 (17.8)		
Interorbital width	36.8-39.9 (38.4)	39.9-42.5 (38.7)	36.3-43.2 (39.5)	38.7-46.1 (42.2)	35.9-42.1 (38.3)	36.5-47.9 (39.8)		
Head width <sub>1</sub> at anterior margin of eyes	42.1-44.5 (43.4)	39.8-46.5 (43.0)	42.4-49.6 (45.4)	42.4-49.2 (46.1)	40.9-46.8 (43.8)	39.3-44.9 (42.8)		
Head width <sub>2</sub> at posterior margin of eyes	53.0-55.9 (54.4)	49.3-56.5 (53.1)	55.6-63.5 (59.1)	56.9-62.6 (59.4)	49.4-58.2 (53.8)	53.5-59.3 (56.1)		
Head depth at interorbital region	47.6-50.7 (49.2)	45.4-54.4 (49.4)	49.1-59.2 (53.6)	46.5-57.1 (52.2)	45.7-53.3 (49.0)	47.5-52.8 (50.2)		
Snout width at nostrils	36.1-39.9 (38.0)	30.9-41.1 (38.3)	35.5-47.6 (40.3)	37.3-44.2 (40.7)	36.4-45.0 (40.4)	34.9-38.9 (37.4)		
Snout depth at nostrils	32.5-34.9 (33.7)	30.0-41.1 (34.2)	33.1-41.6 (37.3)	33.5-41.1 (36.9)	29.7-35.1 (32.7)	31.6-37.2 (33.9)		
Length of anterior barbel	8.5-9.6 (9.1)	8.1-14.1 (10.6)	9.8-14.3 (12.7)	12.1-18.7 (14.6)	12.4-20.8 (16.9)	14.7-19.2 (16.8)		
Length of posterior barbel	11.5-12.2 (11.9)	13.1-19.3 (15.4)	14.7-18.5 (16.5)	16.8-25.5 (20.7)	18.4-28.8 (21.9)	18.6-24.8 (22.3)		
Mouth width	27.9-28.6 (28.3)	27.4-34.2 (30.8)	29.5-38.5 (33.3)	28.5-38.3 (33.7)	29.5-37.9 (34.3)	29.2-36.7 (33.8)		







FIG. 3

Last simple dorsal-fin ray of: **a**, *Capoeta tinca*, FFR 718, 139 mm SL, female; **b**, *C. banarescui*, FFR 712, 144 mm SL, female; and **c**, *C. baliki*, FFR 713, 148 mm SL, female.

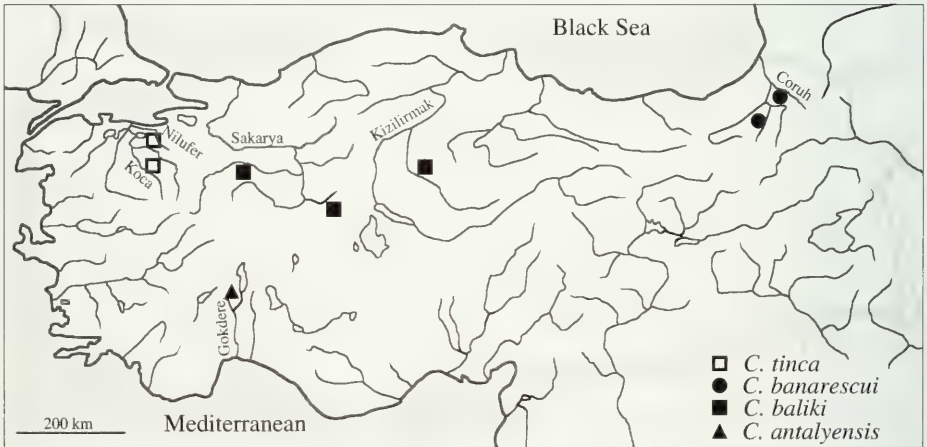


FIG. 4

Distribution of *Capoeta tinca*, *C. banarescui*, *C. baliki* and *C. antalyensis* in Turkey.

**DISTRIBUTION:** *Capoeta tinca* is known from the rivers draining to the southern shore of the Marmara Sea (Fig. 4).

**HABITAT AND BIOLOGY:** *Capoeta tinca* inhabits swift flowing water, with cobbles and pebbles bottom. *Alburnoides bipunctatus*, *Barbus* cf. *oligolepis*, *Barbus* sp., *Chalcalburnus chalcoides*, *Rhodeus sericeus*, *Squalius* cf. *orientalis*, and *Vimba vimba* have been collected together with *C. tinca*.

***Capoeta banarescui* sp. n.**

Fig. 5

*Capoeta tinca* (non Heckel, 1843): Derjugin, 1899 : 155 (in part; Çoruh River, Georgia); Berg, 1914: 0168 (Olty-tchai [Oltu Çayı], Çoruh drainage); Karaman, 1969: 37 (in part; Çoruh drainage; Tortum Reservoir).

*Varicorhinus tinca* (non Heckel, 1843): Berg, 1914: 554 (Çoruh and Rion drainages), 1949: 684 (in part; Çoruh and Rion drainage, Georgia); Elanidze, 1983: 117 (Çoruh, Georgia).

HOLOTYPE: ESFM-PISI/2004-072, 177 mm SL; Turkey: Artvin: Tortum District: Çoruh drainage, stream Tortum, 100 km north of Erzurum; 40°34'N 41°36'E; D. Turan, F. G. Ekmekçi, H. O. Imamoglu, O. Serdar & S. G. Kirankaya, 19 July 2004.

Paratypes. ESFM-PISI/2004-073, 4, 166-201 mm SL; FFR 712, 16, 85-232 mm SL; CMK 18474, 5, 135-193 mm SL; same data as holotype. - FFR 711, 9, 163-231 mm SL; CMK 18540, 9, 121-193 mm SL; Turkey: Artvin: Çoruh drainage, Bulanık stream, Savsat, 30 km east of Artvin, 41°34'N 42°14'E; D. Turan, F. G. Ekmekçi, H. O. Imamoglu, O. Serdar & S. G. Kirankaya, 19 June 2004. - FFR 720, 3, 92-125 mm SL; CMK 18549, 1, 145 mm SL; Turkey: Çavuslu, Borçka, 41°21'N 41°42'E; D. Turan, 13 October 2004.

DIAGNOSIS: *Capoeta banarescui* is distinguished from the other species of the genus by the combination of the following characters: two pairs of barbels; snout pointed; 64-77 lateral line scales; 12-14 rows of scales between lateral line and dorsal-fin origin, 9-11 between lateral line and anal-fin origin; 12-16 gill rakers on first gill arch; shape of lower jaw not sexually dimorphic; head length 22.2-25.8% SL; depth of caudal peduncle 9.8-11.7% SL; head width at posterior margin of eye 49.4-58.2% HL; snout depth at nostril 29.7-35.1% HL; length of anterior barbel 12.4-20.8% HL and posterior barbel 18.4-28.8% HL.

DESCRIPTION: See Figure 5 for general appearance and Tables 1-2 for morphometric and meristic data. Dorsal head profile convex. Snout pointed, rounded in ventral view, depth smaller than width at nostrils. Mouth large and slightly arched, shape not sexually dimorphic (Fig. 6). Rostral fold well developed, partly hiding upper lip. Middle part of upper lip thick, thinner at corners. Upper and lower lips adnate to jaws, lower jaw covered with horny sheath. Tubercles on lower half of body smaller, denser and larger on lower half of caudal peduncle. A row of large tubercles along branched anal-fin rays. Anterior barbel reaching to below anterior margin of eye, beyond corner of mouth. Posterior barbel reaching beyond middle of eye. Predorsal profile of body convex. Body slightly compressed laterally.

Dorsal fin with 3 or 4 simple and 7-9 (modally 8) branched rays, outer margin straight or slightly emarginate, origin markedly in front of vertical through pelvic-fin origin, last simple dorsal ray weakly ossified, flexible and with 12-20 serrae on posterior margin (Fig. 3b). Pectoral fin with 17-19 branched rays. Pelvic fin with 1 simple and 9-10 branched rays. Anal fin with 3 simple and 5 branched rays, outer margin convex. Caudal fin long and deeply forked. Gill rakers large and rounded, 3-5 + 1 + 8-10 = 12-16 on outer side of first arch, number increasing with size (12, in 2 specimens about 80 mm SL; 13, in 2 specimens about 100 mm SL; 14, in 4 specimens 94-135 mm SL; 15, in 11 specimens 125-154 mm SL; 16, in 6 specimens 143-215 mm SL, including holotype). 64-77 lateral line scales, 12-14 scale rows between dorsal-fin origin and lateral line and 8-9 between anal-fin origin and lateral line. 45-46 (modally 45) total vertebrae.

SEXUAL DIMORPHISM: Males collected in July have well developed tubercles on side and tip of snout, and on cheeks.



FIG. 5

*Capoeta banarescui*, holotype, ESFM-PISI/2004-072, 177 mm SL; Turkey: Çoruh drainage: Tortum.



FIG. 6

*Capoeta banarescui*, FFR 712, female, 192 mm SL (left) and male, 178 mm SL (right).

**COLORATION:** Formalin preserved specimens dark brown on back, flank brown, belly yellowish. Each scale margined by a band of black pigments, forming a regular reticulated pattern. Dorsal, caudal and pectoral fins brown; pelvic and anal fins whitish. In life: back and upper flank brownish grey, belly whitish to yellow.

**DISTRIBUTION:** *Capoeta banarescui* is presently known only from the Çoruh (Tchorok) River drainage (Fig. 4). The Çoruh originates from the Kaçkar Mountains in Turkey, but its lowermost course is in Georgia and it flows to the Black Sea at Batumi.

**HABITAT AND BIOLOGY:** *Capoeta banarescui* is known from swift flowing water, with cobbles and pebbles bottom. In June 2004, the temperature was 15-16°C, dissolved oxygen 8.23 mg l<sup>-1</sup>, pH 7.19, and conductivity 125 mS. *Alburnoides bipunctatus*, *Barbus tauricus* and *Oxyinoemacheilus* sp. were collected together with *C.*



*banarescui*. Solak (1982) and Yıldırım & Aras (2000) report that *C. banarescui* spawns between May and July in Çoruh. Males collected in May and June have tubercles on the snout and the body. *Capoeta banarescui* feeds mainly on phytoplankton, zooplankton, some invertebrate, algae and other aquatic plants. In stream Oltu, *C. banarescui* reaches 400 mm (fork length), 838 g and 12 years; it reaches sexual maturity at 2-3 years (Yıldırım & Aras, 2000).

ETYMOLOGY: The new species is named for Petru Banarescu, in appreciation for his contributions to the knowledge of the Turkish fish fauna.

***Capoeta baliki* sp. n.**

Fig. 7

*Varicorhinus tinca* (non Heckel, 1843): Kosswig & Battalgil, 1942: 56 (Ankara).

*Capoeta tinca* (non Heckel, 1843): Erk'akan, 1981: 144 (Sakarya River).

HOLOTYPE: ESFM-PISI/2004-74, 202 mm SL; Turkey: Ankara: Sakarya River: Kızılcahamam Stream, Kızılcahamam, 60 km west of Ankara, 40°29'N 32°39'E; D. Turan & M. Turan, 15 April 2004.

PARATYPES: ESFM-PISI/2004-75, 4, 140-190 mm SL; FFR 713, 5, 121-219 mm SL; CMK 18541, 10, 128-188 mm SL; same data as holotype. - FFR 714, 5, 151-209 mm SL; Turkey: Ankara: Sakarya River, Ova Stream, Kazan, 50 km west of Ankara, 40°11'N 32°39'E; D. Turan & M. Turan, 15 April 2004. - FFR 715, 5, 121-183 mm SL; same data, 16 June 2004. - FFR 716, 10, 168-217 mm SL; Turkey: Sivas: Kızılırmak River, Delice Stream; F. G. Ekmekçi & S. G. Kirankaya, 22 November 2002.

DIAGNOSIS: *Capoeta baliki* is distinguished from the other species of the genus by the combination of the following characters: two pairs of barbels; snout bluntly rounded; 72-86 lateral line scales; 14-17 scales rows between lateral line and dorsal-fin origin, 10-11 (modally 10) between lateral line and anal-fin origin; 16-22 gill rakers on the first gill arch; lower jaw slightly arched in males, straight in females; head length 21.9-24.8% SL; depth of caudal peduncle 9.5-12.3% SL; head width at posterior margin of eye 55.6-63.5% HL; snout depth at nostril 33.1-41.6% HL; length of anterior barbel 9.8-18.7% HL and posterior barbel 14.7-25.5% HL.

DESCRIPTION: See Figure 7 for general appearance and Tables 1-2 for morphometric and meristic data. Dorsal body profile straight. Snout bluntly rounded, rounded in ventral view, depth slightly smaller than width at nostrils. Mouth wide, shape sexually dimorphic, moderately arched in male, straight in female (Fig. 8). Rostral fold weakly developed, partly hiding upper lip. Upper and lower lips adnate to jaws, lower jaw covered with horny sheath. In males collected in April, tubercles on side and tip of snout. Anterior barbel reaching base of posterior barbel. Posterior barbel reaching to below anterior margin of eye. Predorsal profile of body only slightly convex. Body not compressed laterally.

Dorsal fin with 3 or 4 simple and 8-9 (modally 8) branched rays, outer margin slightly emarginate, origin in front of vertical through pelvic-fin origin, last simple dorsal ray weakly ossified, rigid on about two thirds of its length and with 17-23 serrae on posterior margin (Fig. 3c). Pectoral fin with 17-20 branched rays. Pelvic fin with 1 simple and 9-10 branched rays. Anal fin with 3 simple and 5 branched rays, outer margin convex. Caudal fin long and deeply forked. Gill rakers 5-7 + 1 + 10-14 = 16-22 on outer side of first arch, number increasing with size (16, in 2 specimens about 116 mm SL; 17, in 5 specimens about 134 mm SL; 18, in 4 specimens about 155 mm



FIG. 7

*Capoeta baliki*, holotype, ESFM-PISI/2004-74, 202 mm SL; Turkey: Sakarya drainage: Kızılc-ahamam.



FIG. 8

*Capoeta baliki*, FFR 714, female, 176 mm SL (left) and male, 164 mm SL (right).

SL; 19-22, in 24 specimens 173-213 mm SL, including holotype). 72-86 lateral line scales, 14-17 between dorsal-fin origin and lateral line and 10-11 between anal-fin origin and lateral line. 43-44 (modally 44) total vertebrae.



FIG. 9

*Capoeta antalyensis*, FFR 719, 196 mm SL; Turkey: Gökdere stream.



FIG. 10

*Capoeta antalyensis*, FFR 719, female, 149 mm SL (left) and male, 181 mm SL (right).

**SEXUAL DIMORPHISM:** Males with breeding tubercles on snout. Mouth slightly arched in male, straight in female.

**COLORATION:** Formalin preserved specimens dark brown on back, flank brown, belly yellowish brown. Each scale margined by a band of black pigments, forming a regular reticulated pattern. Dorsal, pectoral and caudal fins brown, pelvic and anal fins light brown. In life: back and upper flank brown, belly yellow; caudal, pectoral and pelvic fins dark brown, anal and dorsal fins pale brown.



**DISTRIBUTION:** *Capoeta baliki* is presently known from the Sakarya and Kızılırmak river drainages, including in lakes and reservoirs (Fig. 4). The Sakarya River originates from western central Anatolia and it enters the Black Sea at Sakarya. Kızılırmak River flows from eastern central Anatolia and enters the Black Sea at Samsun.

**HABITAT AND BIOLOGY:** *Capoeta baliki* inhabits slowly flowing water, with cobbles and pebbles substrate. It is also found in lakes and reservoirs, for example Sarıyar Reservoir on Sakarya River (Ekmekçi, 1996) and Gelingüllü Reservoir in Kızılırmak basin (Ekmekçi & Kırankaya, 2004). *Alburnoides bipunctatus*, *Barbus* sp., *Capoeta sieboldi*, *Chalcalburnus chalcoides*, *Squalius* cf. *orientalis*, *Barbatula angorae*, *Oxynoemacheilus* cf. *banarescui* were collected together with *C. baliki*. Males collected in June and July have tubercles on the snout. The spawning period in central Anatolia is in May and June. Sexual maturity is reached 2 years for males and 3 years for females (Ekmekçi, 1996; Ekmekçi & Özeren, 2002). *Capoeta baliki* reaches 428 mm (fork length), 1178 g and 10 years (Yılmaz, 1994).

**ETYMOLOGY:** Named for Süleyman Balık, for his contributions to the knowledge of the Turkish fish fauna.

## DISCUSSION

Species of *Capoeta* have (and still are) often placed in the genus *Varicorhinus*, together with a number of very different cyprinids from Africa, South and Southeast Asia. The type species of *Varicorhinus* is an African fish and the name is correctly used only for African species. The genus *Capoeta* was last revised by Karaman (1969) who recognized seven valid species: *C. tinca*, *C. fusca*, *C. pestai*, *C. buhseri*, *C. capoeta*, *C. trutta* and *C. barroisi*. Banarescu (1999) redescribed some of the species recorded from Turkey and noted problems with the identification of some populations. *Capoeta banarescui* and *C. baliki* are immediately distinguished from most other species of *Capoeta* in having two pairs of barbels, a character shared only with *C. tinca* and *C. antalyensis*.

*Varicorhinus tinca* was described by Heckel (1843) from Bursa (40°15'N 28°55'E), in the Nilüfer drainage. The Nilüfer is a short coastal stream in northwestern Anatolia, draining to the Sea of Marmara. Banarescu & Herzig-Straschil (in Banarescu, 1999) comment that the distribution of *C. tinca* is disjunct and includes most rivers draining to the Sea of Marmara and the Black Sea basins between the Nilüfer and the Sakarya drainages in Anatolia on the one hand and the Tchörök [Çoruh] drainage in western Transcaucasia on the other hand. They mention that the Transcaucasian population does not show variability (which relates with its small range and presence in a single drainage). They report considerable differences between the Transcaucasian and the Anatolian populations. These differences include the number of scale in the lateral line, which they record as 67-80 in the Çoruh population and 72-87 in the western and Central Anatolian populations (but they do not provide separate values for the different drainages in this second area). Their data on the Çoruh population (their Transcaucasian population) is based on at least 6 specimens from Tortum Reservoir examined by them and 22 specimens from an unknown location from Elanidze (1983). It is not known if

the data were obtained by the same methods. Banarescu & Herzig-Straschil concluded that the two groups of populations represent different subspecies but they did not name the Çoruh one. Examination of our material confirms that they are distinct. They satisfy the criteria of species under the Evolutionary Species Concept (ESC) as they are diagnosable and constitute a distinct lineage (Mayden, 2002; Kottelat, 1997).

Our comparison of material from the Çoruh, Kızılırmak, Sakarya, Koca and Nilüfer rivers shows that the Çoruh material (*C. banarescui*) is immediately distinguished from all others by the absence of sexual dimorphism in the shape of the mouth. In *C. banarescui*, the mouth is regularly arched in both sexes (Fig. 6), while in the other species the male has a small, arched mouth, with the edge of the lower jaw rounded, while the female has a broad, straight mouth, with the edge of the lower jaw sharp (Figs 2, 8). *Capoeta banarescui* also has fewer scale rows between the lateral line and the dorsal-fin origin (12-14, mean 12.8, vs. 14-17, mean 15.7 in *C. tinca*, 14-17, mean 14.9 in *C. baliki*) and the anal-fin origin (8-9, mean 8.1, vs. 9-11, mean 9.5 in *C. tinca*, 10-11 mean 10.1 in *C. baliki*), and fewer serrae along the posterior margin of the last simple dorsal-fin ray (12-20, mean 16.0, vs. 24-28, mean 26.6 in *C. tinca*, 17-23, mean 19.5, in *C. baliki*).

Comparison of the material from the Marmara Sea basin (Nilüfer and Koca drainages) and the southern Black Sea Basin (Sakarya and Kızılırmak drainages) also shows that they are specifically distinct. The type locality of *C. tinca* is Nilüfer River and the species from the Marmara basin retains the name *C. tinca*.

*Capoeta banarescui* is further distinguished from *C. tinca* by its more pointed snout (vs. blunt and rounded). It further differs from *C. tinca* in having fewer gill rakers on the first gill arch (12-16, mean 14.7, vs. 19-23, mean 20.6), fewer lateral line scales (64-77, mean 70.8, vs. 69-80, mean 74.9), a somewhat more slender caudal peduncle (depth 9.8-11.7% SL, mean 10.7, vs. 10.8-13.4, mean 11.7), a smaller pelvic-anal distance (18.5-23.6% SL, mean 21.5, vs. 20.9-26.2, mean 23.6), a smaller snout depth at level of nostrils (29.7-35.1% HL, mean 32.7, vs. 30.0-41.1, mean 34.1), longer anterior (12.4-20.8% HL, mean 16.9, vs. 8.1-14.1, mean 10.6) and posterior barbels (18.4-28.8% HL, mean 21.9, vs. 11.5-19.3, mean 15.2), and a wider mouth (29.5-37.9% HL, mean 34.3, vs. 27.4-34.2, mean 30.6).

*Capoeta banarescui* is further distinguished from *C. baliki* by its more pointed snout (vs. blunt and rounded), in having fewer gill rakers on the first gill arch (12-16, mean 14.7, vs. 16-22, mean 19.3), fewer lateral line scales (64-77, mean 70.8, vs. 72-86, mean 78.4), more vertebrae (45-46, vs. 43-44), a somewhat smaller pelvic-anal distance (18.5-23.6% SL, mean 21.5, vs. 20.5-25.4, mean 23.3), a narrower head (at posterior margin of eye (49.4-58.2% SL, mean 53.8, vs. 55.6-63.6, mean 59.2), and a smaller snout depth at level of nostril (29.7-35.1% HL, mean 32.7, vs. 33.1-41.6, mean 37.2).

*Capoeta baliki* is distinguished from *C. tinca* by having fewer serrae along the posterior margin of the last simple dorsal-fin ray (17-23, mean 19.5, vs. 24-28, mean 26.6), modally fewer scale rows between the lateral line and the dorsal-fin origin (14, vs. 16), fewer vertebrae (43-44, modally 44, vs. 44-46, modally 45), the head shorter (length 21.8-24.5% SL, mean 23.6, vs. 23.3-26.7, mean 24.9) and broader (width at posterior margin of eye 55.6-63.5% HL, mean 59.2, vs. 49.3-56.5, mean 53.1), a some-

what more slender caudal peduncle (depth 9.5-12.2% SL, mean 10.8, vs. 10.8-13.4, mean 11.7), and a much blunter snout (compare Figures 1 and 7).

*Varicorhinus antalyensis* (Fig. 9) was described by Battalgil (1944) from the area of Antalya (on the southwestern coast of Turkey). Among other characters, it is diagnosed by having two pairs of barbels. Karaman (1969) treated *V. antalyensis* as a synonym of *Hemigrammocapoeta kemali* Hanko (1924). Erk'akan & Kuru (1983) collected *Capoeta* specimens in Aksu and Köprü streams near Antalya which they identified as *V. antalyensis*. They compared them with *H. kemali* and concluded that they are not conspecific and that *C. antalyensis* is a valid species. We examined 25 specimens from Gökdere stream (37°24'N 31°11'E) near Antalya which we identify as *C. antalyensis*. They are immediately distinguished from *C. banarescui*, *C. baliki* and *C. tinca* in having fewer lateral line scales (51-57), fewer scales in tranverse line (10-12/7) and no serration along posterior margin of last simple dorsal-fin ray. In *C. antalyensis* too, the shape of the mouth is sexually dimorphic; the male has a small, arched mouth, with the edge of the lower jaw rounded, while the female has straight mouth (Fig. 10).

## COMPARISON MATERIAL

*Capoeta antalyensis*: FFR 719, 10, 78-236 mm SL; CMK 18522, 6, 108-184 mm SL; Turkey: Antalya: Gökdere Stream, 40°29'N 32°39'E; D. Turan, Z. Turan & S. Engin, 9 September 2004.

## ACKNOWLEDGEMENTS

We are pleased to thank Serife Gülsün Kırankaya and Osman Serdar for their help in the field and Semih Engin for figures.

## REFERENCES

- BALIK, S. 1979. Batı Anadolu tatlısu balıklarının taksonomik ve ekolojik özellikleri üzerine araştırmalar [Taxonomical and ecological investigations upon freshwater fishes of Western Anatolia]. *Ege Üniversitesi Fen Fakültesi İlmî Raporlar Serisi* 236: 1-69 [In Turkish].
- BANARESCU, P. M. 1999. The freshwater fishes of Europe. 5. Cyprinidae 2. Part I. *Rhodeus* to *Capoeta*. Aula, Wiesbaden, 426 pp.
- BATTALGIL, F. 1944. Nouveaux poissons des eaux douces de la Turquie. *İstanbul Üniversitesi Fen Fakültesi Mecmuası, Seri B, Tabii İlimler* 9: 126-133.
- BERG, L. S. 1912-14. [Faune de Russie et des pays limitrophes. Poissons (Marsipobranchii et Pisces). Vol. 3. Ostariophysi]. *Izdatelstvo Akademii Nauk, St-Petersburg*, 1 (1912): 1-336, 2 pls, 2 (1914): 337-704, 4 pls. [In Russian].
- BERG, L. S. 1948-49. [Freshwater fishes of the U.S.S.R. and adjacent countries]. *Izdatelstvo Akademii Nauk SSSR, Moskva & Leningrad*, vol. 1 (1948), vols 2-3 (1949). [In Russian; translation: Israel Program for Scientific Translations, Jerusalem, 1965].
- DERJUGIN, K. M. 1899. On the ichthyofauna of southwest Transcaucasia. *Ezhgodnik Zoologicheskogo Muzeia Imperatorskoi Akademii Nauk [Annuaire du Musée Zoologique de l'Académie Impériale des Sciences de St-Petersbourg]* 1899: 148-171 [not seen, from Berg, 1949].
- EKMEKÇİ, F. G. 1996. [Some of the growth and reproduction properties of *Capoeta tinca* (Heckel, 1843) in Sarıyar Dam Lake (Ankara)]. *Turkish Journal of Zoology* 20: 117-126 [in Turkish].



- EKMEKÇİ, F. G. & KIRANKAYA, S. G. 2004. Determination of variation in fish growth during reservoir ontogeny: a case study of the mirror carp population in Gelingüllü Dam Lake (Yozgat,Turkey). *Turkish Journal of Veterinary and Animal Sciences* 28: 1129-1135.
- EKMEKÇİ, G. & ÖZEREN, C. 2003. Reproductivite biology of *C. tinca* in Gelingüllü Reservoir, Turkey. *Folia Zoologica* 52: 323-328.
- ELANIDZE, R. F. 1983. Ichthyofauna in the rivers and lakes of Georgia. *Metzniereva, Tbilisi*, 139 pp. [not seen; from Banarescu, 1999].
- ERK'AKAN, F. 1981. Sakarya havzası balıklarının (Pisces) sistematigi ve biyo-ekolojik ilişkileri üzerine araştırmalar [Studies on systematics and bioecology of fishes (Pisces) of Sakarya Basin]. *PhD Thesis, Hacettepe Üniversitesi, Ankara*, 144 pp. [in Turkish].
- ERK'AKAN, F. & KURU, M. 1983. Re-discussion of systematical status of *Varicorhinus antayensis* Battalgil, 1944. *Hacettepe Bulletin of Natural Sciences and Engineering* 12: 49-65.
- GÜNTHER, A. 1868. Catalogue of the fishes in the British Museum. Vol. 7. *British Museum, London*, XX + 512 pp.
- HANKO, B. 1924. Fische aus Klein-Asien. *Annales Historico-naturales Musei Nationalis Hungarici* 21: 137-158, pl. 3.
- HECKEL, J. J. 1843. Ichthyologie (pp. 991-1099). In: RUSSEGGER, J. Reisen in Europa, Asien und Afrika mit besonderer Rücksicht auf die naturwissenschaftlichen Verhältnisse der betreffenden Länder, unternommen in den Jahren 1835 bis 1841. Erster Band. Reise in Griechenland, Unteregypten, im nördlichen Syrien und südöstlichen Kleinasien. *Schweizerbart, Stuttgart*, Teil 2: 472-1102.
- HUBBS, C. L. & LAGLER, K. F. 1947. Fishes of the Great Lakes region. *Cranbrook Institute of Science, Bulletin* 26: i-xi, 1-186.
- KARAMAN, M. S. 1969. Süsswasserfische der Türkei. 7. Teil. Revision Kleinasiatischen und Vorderasiatischen Arten des Genus *Capoeta* (*Varicorhinus*, partim). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 66: 17-54, pls 1-6.
- KOSSWIG, C. & BATTALGIL, F. 1942. Beiträge zur Türkischen Faunengeschichte I. Süsswasserfische. *Türk Fizikî ve Tabii İlimler Sosyitesi Yıllık Bildirigleri ve Arsivi [Compte Rendu Annuel de la Société Turque des Sciences Physiques et Naturelles]* 8: 32-60.
- KOTTELAT, M. 1997. European freshwater fishes. An heuristic checklist of the freshwater fishes of Europe (exlusive of former USSR), with an introduction for non-systematists and comments on nomenclature and conservation. *Biologia (Bratislava)* 52 (Suppl. 5): 1-271.
- KURU, M. 1975. Dicle-Fırat, Kura-Aras, Van Gölü ve Karadeniz havzası tatlısularında yaşayan balıkların (Pisces) sistematik ve zoocoğrafik yönden incelenmesi [Systematics and zoogeographical study of fishes (Pisces) living in Tigris-Euphrates, Kura-Araxes, Van Lake and Blacksea basins]. *Thesis, Atatürk Üniversitesi, Fen Fakültesi, Erzurum*, 181 pp. [in Turkish].
- KUTRUP, B. 1994. Trabzon yöresindeki tatlısu balıklarının taksonomik ve ekolojik yönden incelenmesi [Taxonomic and ecological study of freshwater fish in Trabzon region]. *PhD Thesis, Karadeniz Teknik Üniversitesi, Fen Bilimleri Enstitüsü, Trabzon*, 64 pp. [in Turkish].
- MAYDEN, R. L. 2002. On biological species, species concepts and individuation in the natural world. *Fish and Fisheries* 3: 171-196.
- SOLAK, K. 1982. Çoruh ve Aras havzasında yaşayan siraz balıklarının (*Capoeta* sp.) biyoloji ve ekolojileri üzerinde araştırmalar [Studies on biology and ecology of siraz fishes (*Capoeta* sp.) living in Çoruh and Araxes basins]. *Thesis, Atatürk Üniversitesi, Temel Bilimler ve Yabancı Diller Yüksek Okulu, Erzurum*, 135 pp. [in Turkish].
- STEINDACHNER, F. 1897. Bericht über die von Dr. Escherich in der Umgebung von Angora gesammelten Fische und Reptilien. *Denkschriften der Kaiserlichen Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Classe*, Abt. 1, 40: 685-699, 3 pls.
- YILDIRIM, A. & ARAS, S. 2000. Some reproduction characteristics of *Capoeta tinca* (Heckel, 1843) living in the Oltu Stream of Çoruh Basin. *Turkish Journal of Zoology* 24: 95-102.



- YILMAZ, M. 1994. Kapulukaya Baraj Gölü (Kırıkkale) 'nde yasayan sazan (*Cyprinus carpio* L., 1758) ve in balığı (*Capoeta tinca* Heckel, 1843) 'nın biyo-ekolojik özellikleri [Bioecological properties of carp sazan (*Cyprinus carpio* L., 1758) and (*Capoeta tinca* Heckel, 1843) living in Kapulukaya Reservoir (Kırıkkale)]. *PhD Thesis, Gazi Üniversitesi Fen Bilimleri Enstitüsü, Ankara*, 290 pp. [in Turkish].

# REVUE SUISSE DE ZOOLOGIE

Tome 113 — Fascicule 2

	Pages
Ding YANG, Bernhard MERZ & Patrick GROOTAERT. Descriptions of three new <i>Platypalpus</i> Macquart from Guangdong, China (Diptera, Hybotidae, Tachydromiinae) . . . . .	229-238
Wolfgang SCHAWALLER. New species and records of the genus <i>Basanus</i> Lacordaire (Insecta: Coleoptera: Tenebrionidae) . . . . .	239-246
Wilson R. LOURENÇO & Steven M. GOODMAN. Further considerations regarding the status of <i>Grosphus madagascariensis</i> (Gervais) and <i>Grosphus hirtus</i> Kraepelin, and description of a new species (Scorpiones, Buthidae) . . . . .	247-261
Adrian SMOLIS & Louis DEHARVENG. <i>Vitronura mascula</i> , a new species of Neanurinae (Collembola: Neanuridae) from northern Vietnam, with a key to the species of the genus . . . . .	263-268
Daniel BURCKHARDT & Pavel LAUTERER. The Palaearctic trioizids associated with Rubiaceae (Hemiptera, Psylloidea): a taxonomic re-evaluation of the <i>Trioza galii</i> Foerster complex . . . . .	269-286
Koen MAES. A new species of <i>Diathrausta</i> Lederer, 1863 from Africa (Lepidoptera, Pyraloidea, Crambidae, Spilomelinae) . . . . .	287-290
Dariusz SKARŻYŃSKI. Redescription of <i>Ceratophysella lawrencei</i> (Gisin, 1963) (Collembola: Hypogastruridae) . . . . .	291-296
Dariusz SKARŻYŃSKI & Adrian SMOLIS. Description of <i>Ceratophysella robustiseta</i> sp. n. from greenhouses in England, with notes on synonymy of <i>C. postantennalis</i> Yosii, 1966 and taxonomic status of <i>C. morula</i> Deharveng & Bourgeois, 1991 (Collembola: Hypogastruridae) . . . . .	297-303
Juan Marcos MIRANDE, Gastón AGUILERA & Maria de las Mercedes AZPELICUETA. Nomenclatural note on the genus <i>Nans</i> (Ostariophysi, Characidae) . . . . .	305
Bernard LANDRY, David ADAMSKI, Patrick SCHMITZ, Christine E. PARENT & Lazaro ROQUE-ALBELO. <i>Taygete sphecophila</i> (Meyrick) (Lepidoptera; Autostichidae): redescription of the adult, description of the larva and pupa, and impact on <i>Polistes</i> wasps (Hymenoptera; Vespidae) nests in the Galapagos Islands . . . . .	307-323
Peter SCHUCHERT. The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Capitata Part 1 . . . . .	325-410
Nora KHAMMES, Sovan LEK & Stéphane AULAGNIER. Identification biométrique des deux espèces sympatriques de souris <i>Mus musculus domesticus</i> et <i>Mus spretus</i> en Kabylie du Djurdjura (Algérie) . . . . .	411-419
Davut TURAN, Maurice KOTTELAT, F. Güler EKMEKÇİ & H. Oguz IMAMOĞLU. A review of <i>Capoeta tinca</i> , with descriptions of two new species from Turkey (Teleostei: Cyprinidae) . . . . .	421-436

Ding YANG, Bernhard MERZ & Patrick GROOTAERT. Descriptions of three new <i>Platypalpus</i> Macquart from Guangdong, China (Diptera, Hybotidae, Tachydromiinae) . . . . .	229-238
Wolfgang SCHAWALLER. New species and records of the genus <i>Basanus</i> Lacordaire (Insecta: Coleoptera: Tenebrionidae) . . . . .	239-246
Wilson R. LOURENÇO & Steven M. GOODMAN. Further considerations regarding the status of <i>Grosphus madagascariensis</i> (Gervais) and <i>Grosphus hirtus</i> Kraepelin, and description of a new species (Scorpiones, Buthidae) . . . . .	247-261
Adrian SMOLIS & Louis DEHARVENG. <i>Vitronura mascula</i> , a new species of Neanurinae (Collembola: Neanuridae) from northern Vietnam, with a key to the species of the genus . . . . .	263-268
Daniel BURKHARDT & Pavel LAUTERER. The Palaearctic trioizids associated with Rubiaceae (Hemiptera, Psylloidea): a taxonomic re-evaluation of the <i>Trioza galii</i> Foerster complex . . . . .	269-286
Koen MAES. A new species of <i>Diathrausta</i> Lederer, 1863 from Africa (Lepidoptera, Pyraloidea, Crambidae, Spilomelinae) . . . . .	287-290
Dariusz SKARŻYŃSKI. Redescription of <i>Ceratophysella lawrencei</i> (Gisin, 1963) (Collembola: Hypogastruridae) . . . . .	291-296
Dariusz SKARŻYŃSKI & Adrian SMOLIS. Description of <i>Ceratophysella robustiseta</i> sp. n. from greenhouses in England, with notes on synonymy of <i>C. postantennalis</i> Yosii, 1966 and taxonomic status of <i>C. morula</i> Deharveng & Bourgeois, 1991 (Collembola: Hypogastruridae) . . . . .	297-303
Juan Marcos MIRANDE, Gastón AGUILERA & Maria de las Mercedes AZPELICUETA. Nomenclatural note on the genus <i>Nans</i> (Ostariophysi, Characidae) . . . . .	305
Bernard LANDRY, David ADAMSKI, Patrick SCHMITZ, Christine E. PARENT & Lazaro ROQUE-ALBELO. <i>Taygete sphecophila</i> (Meyrick) (Lepidoptera; Autostichidae): redescription of the adult, description of the larva and pupa, and impact on <i>Polistes</i> wasps (Hymenoptera; Vespidae) nests in the Galapagos Islands . . . . .	307-323
Peter SCHUCHERT. The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Capitata Part 1 . . . . .	325-410
Nora KHAMMES, Sovan LEK & Stéphane AULAGNIER. Biometrical identification of the sympatric mouse species <i>Mus musculus domesticus</i> and <i>Mus spretus</i> in Kabylie du Djurdura (Algeria) . . . . .	411-419
Davut TURAN, Maurice KOTTELAT, F. Güler EKMEKÇİ & H. Oguz IMAMOĞLU. A review of <i>Capoeta tinca</i> , with descriptions of two new species from Turkey (Teleostei: Cyprinidae) . . . . .	421-436



## Revue suisse de Zoologie: Instructions to Authors

The *Revue suisse de Zoologie* publishes papers by members of the Swiss Zoological Society and scientific results based on the collections of the Muséum d'histoire naturelle, Geneva. Submission of a manuscript implies that it has been approved by all named authors, that it reports their unpublished work and that it is not being considered for publication elsewhere. A financial contribution may be asked from the authors for the impression of colour plates and large manuscripts. All papers are refereed by experts.

In order to facilitate publication and avoid delays authors should follow the *Instructions to Authors* and refer to a current number of R.S.Z. for acceptable style and format. Papers may be written in French, German, Italian and English. Authors not writing in their native language should pay particular attention to the linguistic quality of the text.

Manuscripts must be typed or printed (high quality printing, if possible by a laser-printer), on one side only and double-spaced, on A4 (210 x 297 mm) or equivalent paper and all pages should be numbered. All margins must be at least 25 mm wide. Authors must submit three paper copies (print-outs), including tables and figures, in final fully corrected form, and are expected to retain another copy. Original artwork should only be submitted with the revised version of the accepted manuscript.

We encourage authors to submit the revised final text on a disk (3,5"), or on a CD-R, using MS-WORD or a similar software. The text should be in roman (standard) type face throughout, except for genus and species names which should be formatted in *italics* (**bold italics** in taxa headings) and authors' names in the list of references (not in other parts of the text!), which should be formatted in SMALL CAPITALS. LARGE CAPITALS may be used for main chapter headings and SMALL CAPITALS for subordinate headings. Footnotes and cross-references to specific pages should be avoided. Papers should conform to the following general layout:

**Title page.** A concise but informative full title plus a running title of not more than 40 letters and spaces, full name(s) and surname(s) of author(s), and full address(es) including e-mail address(es) if possible.

**Abstract.** The abstract is in English, composed of the title and a short text of up to 200 words. It should summarise the contents and conclusions of the paper and name all newly described taxa. The abstract is followed by up to 10 keywords, separated by hyphens, which are suitable for indexing. Some of the terms used in the title may be omitted from the list of keywords in favour of significant terms not mentioned in the title.

**Introduction.** A short introduction to the background and the reasons for the work.

**Material and methods.** Sufficient experimental details must be given to enable other workers to repeat the work. The full binominal name should be given for all organisms. The International Code of Zoological Nomenclature must be strictly followed. Cite the authors of species on their first mention.

**Results.** These should be concise and should not include methods or discussion. Text, tables and figures should not duplicate the same information. New taxa must be distinguished from related taxa. The abbreviations gen. n., sp. n., syn. n. and comb. n. should be used to distinguish all new taxa, synonyms or combinations. Primary types must be deposited in a museum or similar institution. In taxonomic papers the species heading should be followed by synonyms, material examined and distribution, description and comments. All material examined should be listed in similar, compact and easily intelligible format; the information should be in the same language as the text. Sex symbols should be used rather than "male" and "female" (text file: \$ = ♂, £ = ♀).

**Discussion.** This should not be excessive and should not repeat results nor contain new information, but should emphasize the significance and relevance of the results reported.

**References.** The author-date system (name-year system) must be used for the citation of references in the text, e.g. White & Green (1995) or (White & Green, 1995). For references with three and more authors the form Brown *et al.* (1995) or (Brown *et al.*, 1995; White *et al.*, 1996) should be used. In the text authors' names have to be written in standard type face. However, in the list of references they should be formatted in SMALL CAPITALS (see below). The list of references must include all publications cited in the text and only these. References must be listed in alphabetical order of authors, in the case of several papers by the same author, the name has to be repeated for each reference. The title of the paper and the name of the journal must be given in full in the following style:

PENARD, E. 1888. Recherches sur le *Ceratum macroceros*. *Thèse, Genève*, 43 pp.

PENARD, E. 1889. Etudes sur quelques Héliozoaires d'eau douce. *Archives de Biologie* 9: 1-61.

MERTENS, R. & WERMUTH, H. 1960. Die Amphibien und Reptilien Europas. *Kramer, Frankfurt am Main*, XI + 264 pp.

HANDLEY, C. O. Jr 1966. Checklist of the mammals of Panama (pp. 753-795). In: WENZEL, R. L. & TIPTON, V. J. (eds). *Ectoparasites of Panama. Field Museum of Natural History, Chicago*, XII + 861 pp.

**Tables.** These should be self-explanatory, not integrated in the text-file, with the title at the top, organised to fit 122 x 180 mm, each table on a separate sheet and numbered consecutively.

**Figures.** These may be line drawings or half tones, not integrated in the text-file, and all should be numbered consecutively. Figures should be arranged in plates which can be reduced to 122 x 160 mm. Drawings and lettering should be prepared to withstand reduction. Magnification should be indicated with scale lines. Authors should refrain from mixing drawings and half tones. If possible, originals of figures (ink drawings, photographs, slides) should be submitted (together with the revised version of the accepted manuscript). Original drawings will not be returned automatically. The *Revue suisse de Zoologie* declines responsibility for lost or damaged slides or other documents. If electronically scanned figures are submitted on disk or CD-R (never in MS-Powerpoint format!), this should be clearly indicated on the print-out of these figures enclosed with the print-out of the text. The following minimum resolutions should be respected: scanned line drawings: 600 dpi; photographs: 300 dpi.

**Legends to figures.** These should be typed in numerical order on a separate sheet.

**Proofs.** Only page proofs are supplied, and authors may be charged for alterations (other than printer's errors) if they are numerous.

**Offprints.** The authors receive a total of 25 offprints free of charge; more copies may be ordered at current prices when proofs are returned.

**Correspondence.** All correspondence should be addressed to

Revue suisse de Zoologie, Muséum d'histoire naturelle, CP 6434, CH-1211 Genève 6, Switzerland.

Phone: +41 22 418 63 33 - Fax: +41 22 418 63 01. E-mail: danielle.decrouez@mhn.ville-ge.ch

Home page RSZ: <http://www.ville-ge.ch/musinfo/mhng/page/rsz.htm>



SMITHSONIAN INSTITUTION LIBRARIES



3 9088 90053 8315